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RECENT CONTRIBUTIONS TO PLANT EVOLUTION

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THE past decade has seen a marked advance in our knowledge of the early history of the vascular plants, especially the discovery in the Devonian of a number of very simple, generalized forms which seem to foreshadow the more specialized pteridophytes of the later Devonian and Carboniferous, and through these the ancestors of the modern floras.[1] These discoveries have aroused a new interest in the phylogeny of the vascular plants, and this is shown by the recent publication of two important contributions to these problems.[2]

The "vascular" plants comprise the pteridophytes—ferns, etc., and the seed-plants, "spermatophytes." These are the predominant plants of the present day. Remains of vascular plants are first encountered in the lower Devonian rocks.

There is pretty general agreement that the ancestors of the higher plants were aquatic organisms, similar to some of the algae still living; but how the first land-plants arose from their algal ancestors is a matter of much controversy.

[1] Lang, "Contributions to the Study of the Old Red Sandstone Flora of Scotland," Trans. Roy. Soc. Edinb., Vol. 54, 1925; R. Kräusel and H. Weyland. Beiträge zur Kenntnis der Devonflora. Abhand. Senck. Naturforsch. Gesellsch. 40, II. 1924.

[2] A. C. Seward, "Plant Life through the Ages." Cambridge University Press. 1931; W. Zimmermann, "Die Phylogenie der Pflanzen." Jena, 1930.

In all typical plants with sexual reproduction there is an "alternation of generations." The sexual cells, "gametes," unite to form a "zygote," whose nucleus has double the number of chromosomes found in the gametes, *i.e.*, is diploid. The complicated plants we know as the fern or flowering plant is the product of the continued growth and differentiation of the unicellular zygote resulting from the union of the male and female gametes; and the nuclei of all the cells retain the diploid character of the zygote. In order that the original "haploid" condition may be restored, a peculiar type of nuclear division is necessary, known as a "reduction" division or "meiosis."

The life-cycle of the diploid "sporophyte" is completed by the formation of special reproductive cells—spores. These are formed in tetrads from special cells—"spore mother-cells"—and the first nuclear division of the mother-cell is a reduction division, and the last division results in four spores having the original haploid chromosome number. From these haploid spores the new generation of sexual plants—the gametophytes—arises, producing the gametes from whose union the sporophyte develops.

The question as to whether the highly specialized sporophyte is a modification of the sexual gametophyte, or whether it is an independent neutral structure interpolated between the sexual generations, has aroused much controversy. The writer believes the evidence for the latter theory, *i.e.*, the so-called "antithetic" theory of the alternation of generations, is the more convincing.[3]

In the fern we see the marked difference between the very simple sexual plant and the large and complex neutral generation. From the germinating spore, there develops the minute flat liverwort-like "gametophyte" bearing the sex organs, archegonium and antheridium—this gametophyte is, in short, the sexual phase of the

[3] For a more extended discussion of the subject see the writer's "Mosses and Ferns," 3rd ed., Chap. XV.

fern's life. The female gamete, the egg, contained in the archegonium, is fertilized by the active male gamete—

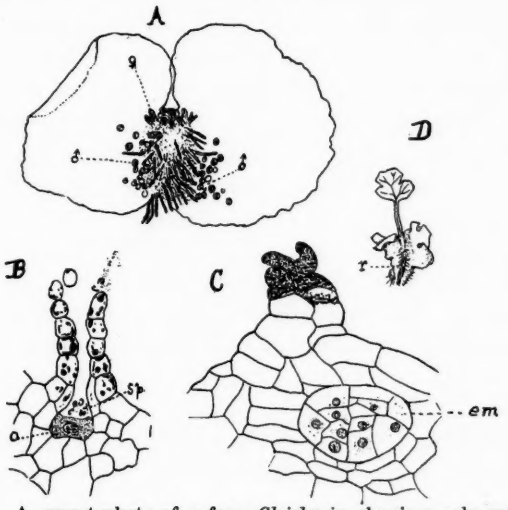

FIG. 1. A, gametophyte of a fern, *Gleichenia,* showing male and female reproductive organs. B, an open archegonium—o, the egg-cell, sp., spermatozoids. C, an embryo, em. D, the young sporophyte attached to the gametophyte, g; r, the primary root.

the spermatozoid. The resulting zygote remains within the archegonium, where it develops into a globular or oval mass of cells, the embryo, which is protected by the surrounding tissue of the gametophyte until it has formed the primary organs of the young fern—stem, leaf and root. By the development of the root, which penetrates the substratum, the young plant no longer is dependent on the gametophyte for its support and the gametophyte usually dies, leaving the little fern rooted in the ground. This is the "sporophyte," which sooner or later produces the spores. As these spores are the product of simple cell-division, *i.e.,* are asexual, the sporophyte represents the non-sexual or neutral phase of the fern's life history.

In all the vascular plants the sporophyte arises in an analogous manner, and this is true also for the liverworts

and mosses where, however, the sporophyte remains permanently connected with the gametophyte, and dies as soon as the spores are shed.

Since the sporophyte of all the higher plants begins as an undifferentiated embryo, in contrast with the green algae where the zygote develops into a simple resting spore, the name "embryophyte" has been proposed to include all the plants above the algae.

Our knowledge of the evolution of the mosses and liverworts is mainly derived from a study of existing species, as the known fossil remains of these plants are very scanty. This is due in part to the delicate tissues of most of them, but the recent discovery of unmistakable liverworts in the Carboniferous suggests that a more intensive search for these delicate plants may reveal something of their geological history.

A comparative study of the development of the sporophyte in the living bryophytes reveals some of the factors which seem to have been concerned in the establishment of the independent sporophyte of the vascular plants.

The simplest known sporophyte is that of certain liverworts of the genus Riccia. The adult sporophyte is a globular capsule filled with spore-tetrads. Throughout its development it is embedded in the gametophyte, from which it derives its nourishment. In short, the sporophyte is completely parasitic. In most liverworts, however, only a part of the embryo is devoted to spore-formation. A special organ, the foot, anchors the young sporophyte in the tissues of the gametophyte, and also acts as a haustorium through which nourishment is supplied to the growing sporophyte. The terminal portion becomes a spore capsule, but some of the sporogenous cells remain undivided and form peculiar elongated cells, elaters, which are concerned with the opening of the capsule and the scattering of the spores. Between the foot and the capsule there is a stalk, "seta," which may attain a length of several centimeters in some cases.

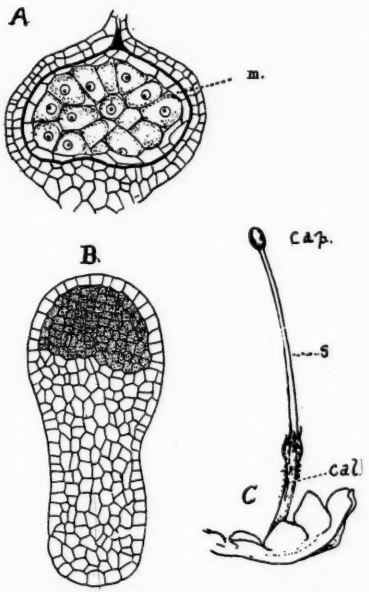

FIG. 2. A, young sporophyte of a liverwort, Riccia, enclosed in the archegonium. All the cells, except the layer, m, develop spores. B, another liverwort, Fimbriaria. The sporogenous tissue is shaded. C, ripe sporophyte of Treubia—the spore capsule borne on a long stalk, s.

The great importance of this "sterilization" of potentially sporogenous tissue in the evolution of the sporophyte has been emphasized by Professor Bower.[4] In all the liverworts the sporophyte remains intimately associated with the gametophyte, and its specialization is concerned with the formation and dissemination of the spores, the sporophytes quickly collapsing after their discharge.

In two classes of bryophytes, however, the sporophyte attains a considerable degree of independence, *viz.*, the Anthocerotes and the true mosses. In both of these the sporophyte may continue to grow for a long period, and attain a relatively large size. This growth is accompanied by a great reduction in the sporogenous tissue,

[4] F. O. Bower, "The Origin of a Land Flora." London, 1908.

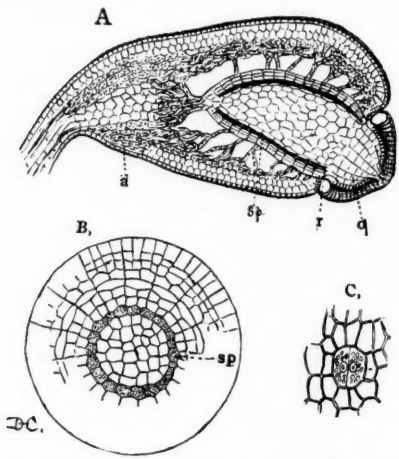

FIG. 3. A, longitudinal section of the spore-capsule of a moss, Funaria. The sporogenous tissue, sp. greatly reduced. B, cross-section of a young sporophyte, showing the single layer of sporogenous cells. C, a stoma from the base of the capsule.

and the development of a large amount of green tissue, by means of which the sporophyte can manufacture carbon compounds needed for its growth. There may be developed also a strand of conducting tissue comparable with the fibro-vascular bundles of the simplest vascular plants.

In some of the true mosses there is developed a very complicated mechanism for discharging the spores, and well-developed conducting tissue, as well as a perfect system of photosynthetic tissues. Nevertheless, there is little indication of a tendency, on the part of the highly specialized sporophyte, which in the mosses attains a complexity quite unmatched among the liverworts, and is adapted to a much greater range of conditions in the environment, to become independent.

In the Anthocerotes, although the sporophyte may reach a size comparable to that of the mosses, and like them has a marked reduction in the amount of sporogenous tissue, and a corresponding increase in the green

tissue, it is much less specialized than that of the mosses. In Anthoceros, the sporophyte is a slender cylindrical green body, with a large foot embedded in the gametophyte. There is no elaborate mechanism for distributing the spores, which may continue to form for months after the first ones are discharged, and the growth of the sporophyte is not checked by the ripening of the first spores. The continued growth is due to the development of a zone of actively dividing cells between the large foot and the upper part of the sporophyte. The foot provides the necessary water for the growth of the sporophyte, while the abundant green tissue manufactures the necessary carbon compounds, through photosynthesis. Were the

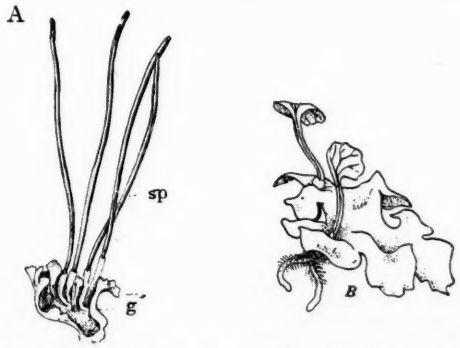

FIG. 4. A, gametophyte of Anthoceros, bearing four sporophytes. B, gametophyte of a fern, Danaea, with two young sporophytes.

foot able to procure water directly from the ground, the sporophyte, like that of the young fern, would no longer need the gametophyte, and indeed in some exceptional instances,[5] such actually seems to be the case. In some of these sporophytes it was significant that in the later formed basal tissue the sporogenous cells were almost wanting, and there was a marked increase in the amount of green tissue. A central core of presumably conducting cells, directly comparable to the primary vascular

[5] D. H. Campbell, "Annals of Botany." July, 1924.

bundle in some of the primitive ferns, replaced the slender columella ordinarily present.

The writer has long maintained that Anthoceros, more than any other known form, suggests what may have been the structure of the first vascular plants. This view has been confirmed by the actual discovery of what, up to the present, are the simplest known true vascular plants.

About sixteen years ago there were discovered in Devonian rocks—the Old Red Sandstone—of Scotland, the petrified remains of what had evidently been a peat-bog.[6] The plant fragments were preserved with extraordinary perfection, and a study of these showed the presence of certain extremely simple plants differing so much from any known forms that a special family, Rhyniaceae, was established to contain them. The perfect petrifaction of these remains enabled a complete study, not only of their external characters, but of their anatomy and even their fructification.

The resemblance in structure between these fossils, and

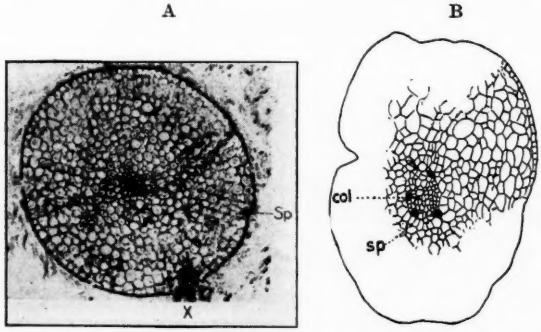

FIG. 5. A, cross-section of the shoot of Rhynia, the simplest known vascular plant, from the Devonian. B, a similar section of the sporophyte of large sporophyte of *Anthoceros fusiformis*. A, after Zimmermann.

the sporophytes of some of the existing Anthocerotes, is quite extraordinary, especially when compared with the large specimens of Anthoceros already mentioned.

[6] R. Kidston and W. H. Lang, "On Old Red Sandstone Plants Showing Structure." Pt. I. Rhynia. Trans. Roy. Soc. Edinb., 51, III, 1917.

The Rhyniaceae include two genera, Rhynia and Hornea. The first species described, *Rhynia Gwynne-Vaughnii,* was a slender leafless plant, sometimes dichotomously branched. The shoot arose from a prostrate rhizome, structurally much like the upright shoots. No roots were present. In size, the smaller specimens scarcely exceeded the largest Anthoceros sporophytes. Sections of the shoot of Rhynia show a central vascular bundle with a core of woody tissue, the rest of the shoot being composed of uniform thin-walled parenchyma. In the more slender shoots the woody tissue may be reduced to two or three tracheids, and in the smallest branches tracheary tissue may be quite absent. Sections of the largest Anthoceros sporophytes show a structure almost identical with that of Rhynia except for the complete absence of woody tissue.

Owing to the permanence of the woody tissues, the vascular bundles are often preserved very perfectly as fossils, and are of great importance in establishing the relationships of many fossil plants. Nevertheless, caution is necessary and it is not always safe to base relationships on woody structures alone. This may be illustrated by a living instance. The two genera, Ophioglossum and Botrychium, are placed by taxonomists in a single family, Ophioglossaceae; yet their stem anatomy is almost as diverse as that of a typical monocotyledon and dicotyledon. On the other hand, among fossils belonging to widely divergent phyla similar vascular bundles are present, *e.g.,* the development of secondary wood in many unrelated forms.

The sporophyte of Rhynia is not very much advanced beyond that of the largest known types of Anthoceros. The plant body had not yet developed the definite organs of the typical vascular plants, *viz.,* stem, leaf and root, but showed the first step in the formation of external organs by the development of dichotomous branches. Zimmermann[7] has proposed for such an undifferentiated

[7] *Loc. cit.,* p. 65.

dichotomously branched plant body the term "telome," and this term is also applied to the ultimate branches of such a telome system. The branches of the telome may be either fertile or sterile.

In Rhynia spores are produced at the apex of some of the branches. The mass of spores is covered by several layers of cells, including the epidermis, and this fertile tip of the branch forms a very primitive sort of sporangium.

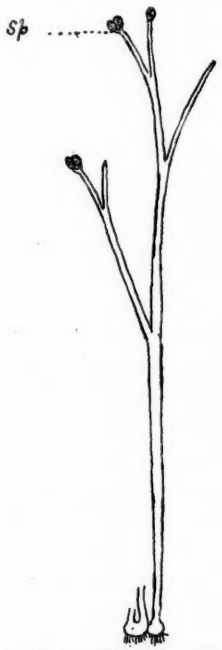

FIG. 6. *Hornea Lignieri.* Restoration after Kidston and Lang. sp. sporangia.

A second genus, Hornea, is much like Rhynia in form, but differs in some particulars. The "rhizome," instead of being elongated, and similar to the upright shoots, is a tuberous body, destitute of any vascular bundle, and strongly suggesting the large foot of the sporophyte of

Anthoceros. An English botanist has described Hornea "As in fact little more than a slightly ramified and free growing Anthoceros."[8] The resemblance to the Anthocerotes is increased by the origin of the sporogenous tissue. A section of the tip of a fertile branch shows that the spores form a thick layer overarching a central mass of sterile tissue, or columella, a condition characteristic of all the Anthocerotaceae. A comparison of a section of Hornea and the simplest of the Anthocerotaceae, Notothylas, where the sporogenous tissue is more abundant than in Anthoceros, is significant.

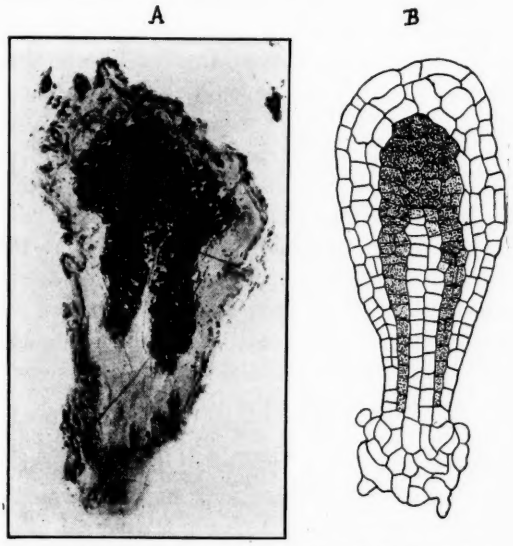

FIG. 7. Longitudinal section of a sporangium of Hornea (A), compared with a similar section of a young sporophyte of Notothylas (B), one of the Anthocerotes. A, after Zimmermann.

From the study of these earliest known vascular plants, and their obvious resemblances to the Anthocerotes, which among the existing bryophytes approach most nearly the independent sporophyte of the pteridophytes,

[8] Seward, *loc. cit.*, p. 30.

it is justifiable to conclude that the ancestors of the first vascular plants were, if not actually Anthocerotes, at any rate were very much like them.

There is strong evidence that the Anthocerotes are very old types. The gametophyte more nearly resembles the green algae than does that of any other Archegoniate. On the other hand, the sporophyte comes nearest to complete independence of any of the bryophytes; and, except for the absence of tracheary tissue and lack of branching, can readily be compared with the undifferentiated "telome" of the Rhyniaceae. It is quite conceivable that, like the still more ancient ancestors of the higher plants, the green algae, the existing Anthocerotes are the little changed descendants of plants that flourished long before the first vascular plants appeared upon the earth.

Other important discoveries of Devonian plants of very primitive structures have been made, which seem to foreshadow the principal classes of living pteridophytes. The most remarkable forms were somewhat more advanced than the Rhyniaceae, but show evident resemblances to them. These have been described in a number of important papers by Professor R. Kräusel, of Frankfurt, and some of his collaborators. These were discovered near Elberfeld in the Rhine Valley.

One of these, Asteroxylon, apparently resembled in habit some of the living species of Lycopodium, and the structure of the vascular cylinder, or stele, was also comparable with that of Lycopodium. Kräusel has figured a restoration of Asteroxylon, which shows upright, much branched shoots arising from a prostrate rhizome, much as in the living club-mosses. Like these, also, the branching was dichotomous. The larger axes were covered with small appendages—perhaps rudimentary leaves—but the terminal shoots were smooth and coiled like the young frond of a fern.

It is quite conceivable that the Asteroxylon type might have come from a form like Rhynia by the development

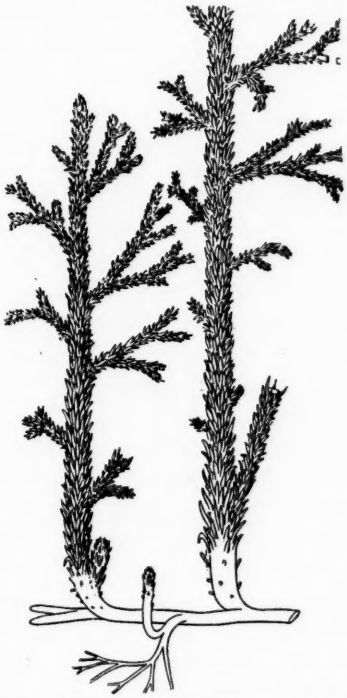

FIG. 8. Asteroxylon, a Devonian fossil, suggesting the living club-mosses. Restoration after Kidston and Lang.

of small superficial leaves, and a further development of the axial fibro-vascular cylinder. It is also conceivable that there may be a real connection between Asteroxylon and the club-mosses (Lycopsida).

One small family of living pteridophytes, the Psilotaceae, show such resemblances to the Rhyniaceae that their inclusion in the same class, Psilophyta, is probably warranted. The Psilotaceae comprise only a few species, one of which, *Psilotum triquetrum,* occurs in most tropical and subtropical regions. The second genus, Tmesipteris, is restricted to the Australasian and Polynesian regions. The upright dichotomously branched shoots of Psilotum are practically leafless and arise from

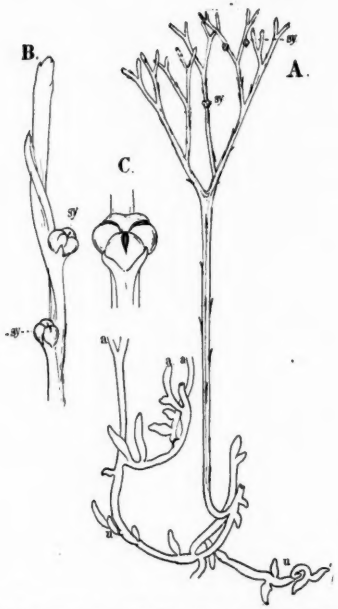

FIG. 9. *Psilotum triquetrum*, probably the nearest living relative of the Devonian Rhyniaceae. After Bertrand.

a rhizome, as in Rhynia, and like Rhynia it is destitute of true roots. The sporangia are in groups of three and are formed at the apex of short special branches. We may consider the Psilotaceae as relicts of an extremely ancient and almost extinct class.

With the fossil Psilophyta are associated many extinct types, which show more or less evident relationship with the three principal classes of living Pteridophytes, *viz.*, the club-mosses, Lycopsida; the fern-alliance, Pteropsida; and the Equisetineae (horsetails), Articulatae.

All three classes can be traced back to the Devonian, and some of the middle Devonian fossils, described by Kräusel and others, might be interpreted as synthetic types connecting the modern ones with forms like the Rhyniaceae.

The differentiation of the plant-body seems to have proceeded along two lines. In one direction the result was a dichotomously branched axis, bearing many small leaves, with a single median vascular bundle. A massive stele occupies the axis of the shoot. This type is exemplified by the living species of Lycopodium, and is characteristic of the class Lycopsida. Among the fossil lycopods are forms closely resembling the living species and probably directly related to them. But from the later Devonian and through the Carboniferous, the Lycopsida developed into trees, of which species of Lepidodendron and Sigillaria are among the most characteristic fossils of the later Paleozoic. The structure of the wood was very much like that of the living conifers, and the leaves were not unlike in structure, and it has even been suggested that these arborescent club-mosses may have been related to the existing conifers, although it must be said this view is not generally accepted.

While there is some evidence for the persistence of a few relatives of these giant club-mosses in the early Mesozoic, they were no longer a dominant feature in the floras, and their place was taken by numerous conifers, which for a long time dominated the Mesozoic forests.

There is abundant evidence that some of the fossil lycopods were heterosporous like the living genus Selaginella; but there were also forms, *e.g.*, Lepidocarpon, in which true seeds were developed, and it is this fact which has suggested that the conifers might be descended from seed-bearing lycopods. Whether or not this theory is correct, the giant lycopods of the Carboniferous became practically extinct by the end of the Paleozoic.

A characteristic of all existing lycopods is the structure of the spermatozoids, which are biciliate, in which respect they agree with the bryophytes, including Anthoceros. Whether or not the Rhyniaceae resembled the lycopods in this important character is, of course, useless to speculate. All the other living pteridophytes, Psilotaceae, ferns and horsetails have large multiciliate sperms, and

on this basis the pteridophytes have been divided into two categories,[9] Biciliatae and Polyciliatae.

We have already seen that the living Psilotaceae show evidences of a real relationship with the Devonian Rhyniaceae; but evidences of a similar relationship with the other Polyciliatae is not so clear. However, some of the recently discovered Devonian fossils may indicate the possibility of a derivation of the Articulatae and Pteropsida from Psilophyta, and also a remote relationship between the horsetails and the lower ferns—a view suggested by the writer many years ago. This conclusion was based upon marked resemblances in the gametophyte and embryo, although the contrast between the hollow-jointed stem and rudimentary leaves of Equisetum and the short solid stem and large and complex fronds of the fern would seem to make any relationship extremely unlikely. However, in the oldest-known examples of the Articulatae, *e.g.,* Asterocalamites, the leaves are much more conspicuous and are repeatedly dichotomous, very much as in many ferns.

In the Rhyniaceae, the forked plant-body (telome) shows both fertile and sterile branches, which have been denominated respectively "sporangiophore" and "phylloid." By repeated dichotomy in one plane, such a plant-body would result in a fan-shaped structure, not yet clearly differentiated into stem and leaf. A flattening of the branches would then result in a fan-shaped frond much like the leaves of many living ferns, *e.g., Schizaea dichotoma,* Dipteris, Matonia.

From a study of the development of the most primitive of the living ferns, it seems probable that in the ancestors of the modern ferns the sporophyte consisted of a single large leaf and a "protocorm" or foot. The root was a later development, arising endogenously and piercing the foot, and forming a much more efficient organ for water absorption.

[9] J. P. Lotsy. Botanische Stammesgeschichte. Vol. 2: 447, 1909.

FIG. 10. Hyenia, a Devonian fossil, perhaps related to the ferns. Restoration after Kräusel and Weyland.

It is possible that such forms as the Devonian Cladoxylon and Hyenia may resemble the predecessors of the modern ferns. Hyenia, according to Kräusel's restoration of this remarkable plant, was a fan-shaped body suggesting the frond of a fern, but the branches were beset with slender dichotomously branched appendages, some of which were sporangiophores having at their apices pendant sporangia, recalling the sporangiophores of Equisetum. The branching of the main plant-body, and the absence of any indication of the jointed axis of Equisetum, is very different from the condition in any of the typical Articulatae. Much resembling Hyenia in general form is another remarkable plant, Calamophyton, also described by Kräusel. Obviously related to Hyenia, it differs in having the main branches distinctly jointed, and from the nodes arose lateral branches, much as in

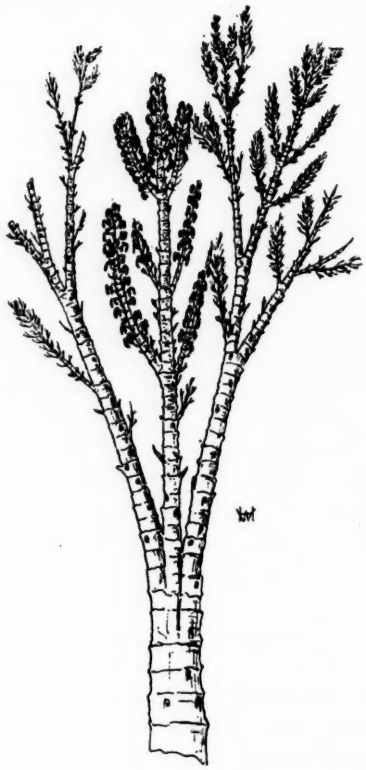

FIG. 11. Calamophyton, a Devonian fossil, showing possible relationship with the horsetails (Equisetineae). Restoration after Kräusel and Weyland.

the living Equisetum. From the nodes of some of the lateral shoots, whorls of small forked leaves comparable to those of Asterocalamites, were present, while from other nodes were produced sporangiophores much like those of Hyenia. In short it is quite conceivable that from forms resembling Hyenia and Calamophyton with their fern-like fronds, there developed in one direction the typically megaphyllous (and primarily monophyllous) ferns, and in another direction, through forms like

Hyenia and Calamophyton, the primitive Asterocalamites where the relatively large leaves retain the primitive dichotomous branching.

With a progressive reduction of the leaves, and a correspondingly increased importance of the axis, we may infer that the condition found in the sole remaining representatives of the class, the genus Equisetum has arisen.

As in the lycopods, it is probable that the living Equisetaceae are the descendants of the less specialized Paleozoic types, while the tree-like Calamites of the Carboniferous and the Sphenophyllales have left no descendants and have given way to the seed-plants. Heterospory has been demonstrated in a few of the Calamites, but no evidence of seeds in any of them has been discovered; and all that remains of the class at the present time is the single genus Equisetum, with some 25 to 30 species.

Of the living ferns there is good reason to believe that the Ophioglossaceae are the most primitive. Unfortunately, perhaps due to their delicate structure, practically nothing is known of their geological history. It is, however, not unlikely that an extinct order of ferns, characteristic of the later Devonian and lower Carboniferous, the Coenopteridales, may have been related to the Ophioglossaceae.

The young sporophyte of *Ophioglossum pedunculosum* (*O. moluccanum*) shows a structure suggestive of Rhynia or Anthoceros.

It consists at first of an apical region, which develops into the primary leaf and a foot; but very early there is formed endogenously near the base of the leaf a root which penetrates the foot and grows vertically into the substratum. The root and leaf are in the same plane, and the young sporophyte is thus distinctly bipolar. There is an axial stele which extends unbroken through root and leaf. Presumably, in the ancestral form, the apical region was sporogenous, but in the living species the development of spores does not take place until a

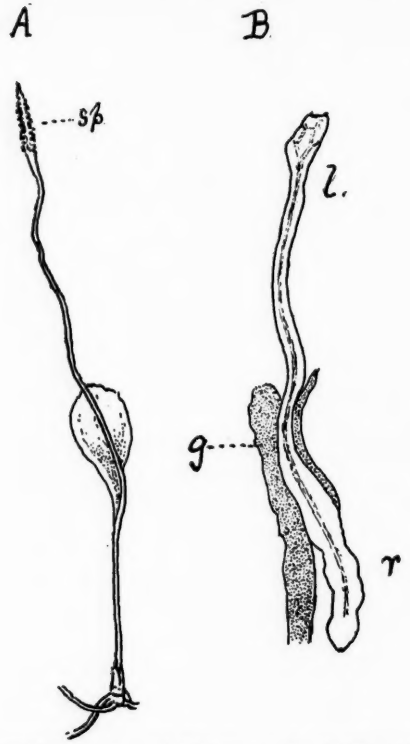

FIG. 12. A, Ophioglossum, probably the most primitive of living ferns, sp. the sporangial spike. B, longitudinal section of the young sporophyte, which consists only of the primary leaf, l, and root, r; g, the gametophyte.

much later period. However, since in *Ophioglossum moluccanum* the spike and sterile leaf segment are the results of a dichotomy of the leaf primordium, it is possible that in the beginning there was a division of a "telome" into a sporangiophore and "phylloid," such as occurs in some of the early Devonian pteridophytes. A similar dichotomy of the primordium of the fertile frond has been reported for *Botrychium lunaria*. We might also consider the possibility of the derivation of the peculiar sporangial spike of Ophioglossum from an an-

cestral type more like Anthoceros than like Rhynia. The solid spike of Ophioglossum, with its two rows of deeply sunken spore-masses, has a certain analogy, at least, with the sporogenous tissue of the Anthocerotes, where there may be quite definite alternation of fertile and sterile areas, suggesting a tendency to the segregation of the fertile sporogenous tissue into distinct masses. There might thus result a series of simple sporangia with individual marginal dehiscence, as in Ophioglossum, rather than the single terminal sporangium of the Rhynia type.

The evolution of the much branched sporangiophore of Botrychium, with its definite sporangia from the solid spike, and sunken sporangia of Ophioglossum, is readily conceivable, and this might possibly be extended to the fertile fronds of Osmunda. It is not so easy, however, to understand the development of the common fern-type with the sporangia borne on the lower side of the frond, although it must be borne in mind that, in the Osmundaceae, Todea has the sporangia on the lower surface of the leaves, much as in the common ferns.

We might perhaps imagine two types of primitive ferns developed from ancestors resembling Anthoceros; one, through intermediate forms like the Psilophtales resulting in a broad dichotomously divided frond with terminal sporangia—like Cladoxylon, the other more directly developing the spike-like sporangiophore of Ophioglossum.

That there must have been many simple fern-like plants before the end of the Devonian is indicated by the occurrence in the latter part of this era of such plants of giant dimensions, which had progressed to the point of seed production. Most remarkable of these was a genus, Eospermatopteris, discovered in eastern New York State.[10] A freshet near Gilboa exposed a great number of large stumps, some of them two feet or more in diameter. Restorations of these plants indicated that they

[10] Winifred Goldring, "The Upper Devonian Forest of Seed-ferns in Eastern New York," *N. Y. State Mus. Bull.*, 251. Albany, 1924.

resembled in general appearance modern tree-ferns, although differing in several important particulars. It is clear that they were not at all closely related to any modern ferns, but nevertheless, they must have had many relatives allied to true ferns.

Eospermatopteris and other fern-like plants which bore seeds are known as pteridosperms, and become a very important element in the Carboniferous floras. Many of the "fern-fronds" of the coal measures are now known to be leaves of pteridosperms. Some of these pteridosperms may have been the ancestors of more perfect seed plants of the later epochs. Of the very numerous fern-like fronds which abound in the Paleozoic from the Devonian onward, it is impossible always to decide whether they belong to true ferns, pteridosperms, or cycads.

The pteridosperms probably do not form a closed phylum, and there is every reason to assume that the development of seeds was attained in many independent lines. It is, therefore, not likely that all the later seed-plants are descended from the same Paleozoic ancestors.

While the seed habit was first developed in the later Devonian, it was during the Carboniferous that the pteridosperms became prominent. Seeds were also developed in some lycopods and in the peculiar order Cordaitales, whose relationships with other seed-plants are not clearly understood. Doubtfully represented in the Upper Devonian, they were abundant through the Carboniferous and Permian, but were practically extinct by the end of the Paleozoic. They were trees of considerable size, suggesting the Kauri pines (Agathis) of the Southern Hemisphere, from which, however, they differed greatly in their reproductive parts. In a way they were generalized types, showing characters suggesting the pteridosperms, conifers and cycads, but their real relationships with any of these phyla are extremely dubious.

It is in the later Carboniferous that the first recognizable ancestors of the most primitive living seed-plants appear. All the Paleozoic seed-plants, as well as their nearest living relatives, are "gymnosperms," *i.e.*, the seeds are borne either on an open leaf, sometimes resembling the foliage leaves, as in Cycas, or on scale-leaves, as in the conifers. More rarely they are borne at the apex of a naked axis—a sporangiophore like that of the primitive pteridophytes. These ancient gymnosperms evidently belong to several independent phyla, and it is clear that the existing gymnosperms represent remnants of several divergent lines of development whose relationships to each other, and to the Paleozoic seed-plants, are very imperfectly understood.

Of the living gymnosperms, two orders—Cycadales and Ginkgoales—show unmistakable evidences of fern ancestry, and presumably have originated from some Paleozoic pteridosperms. Indeed, there are many fossil leaves in the late Carboniferous and Permian which belong either directly to these two orders or to pteridosperms related to them.

Seward,[11] commenting on certain leaf-impressions resembling Ginkgo from Permio-Carboniferous beds, says, "It is difficult to resist the conclusion, though it is based on leaves alone, that this type is a Paleozoic forerunner of the group Ginkgoales." He remarks also, in regard to the cycads,[12] "The probability is these plants appeared before the end of the Carboniferous, but it was not until the latter part of the Triassic they began their rapid progress toward a position of dominance."

The Cycadales and Ginkgoales are undoubtedly the most primitive orders of living seed-plants. Not only do they recall the ferns in the character of their leaves, and especially in the cycads, in their anatomy, but, unique among living seed-plants, fertilization is effected by large ciliated sperms exactly as in typical ferns. From

[11] A. C. Seward, *loc. cit.*, p. 226.

[12] *Ibid.*, p. 281.

a study of certain fossil seeds belonging to pteridosperms and Cordaitales, it is safe to assume that in these extinct types, also, active spermatozoids were developed.

The peculiar maiden-hair tree, *Ginkgo biloba*, long cultivated in China and Japan, and sometimes planted for ornament in America, is the sole living representative of its order—a veritable living fossil. It is quite unknown outside cultivation, but has come down from remote antiquity, apparently little changed from its Paleozoic ancestors. The order was represented by many forms during the Triassic and Jurassic, which became extinct, leaving the living species as the sole survivor of the order.

Like the Ginkgoales, the cycads (Cycadophytes) attained their maximum development in the Mesozoic, especially in the later Triassic and Jurassic, when they played a very important rôle in the vegetation. While many of these were similar to the existing cycads (Cycadales), a second order, now completely extinct, contained many forms, having a more complicated type of inflorescence, which in some cases suggests the flowers of some of the modern flowering plants or angiosperms. This has led some botanists[13] to conclude that the angiosperms have been derived from some of these cycadeoids (Bennettitales).

There are, however, strong objections to this view, based in part upon fundamental differences in the floral structures, and it is hardly likely this theory will be generally accepted. These highly specialized cycadeoids reach their culmination in the Cretaceous and have no living representatives. However, the less specialized Cycadales, some of which, *e.g.*, Cycas, are probably very old types, have about a hundred living species distributed over the warmer parts of the world. In the United States two species of Zamia in southern Florida represent the order.

[13] *E.g.*, E. A. N. Arber and J. Parkin, "On the Origin of the Angiosperms," *Jour. Linn. Soc. Bot.*, 38: 1907.

While the living cycads and Ginkgo are evidently relicts of a flora once much more extensive than at present, the coniferous trees, Coniferales, play a much more important rôle in the vegetation of the modern world. Over extensive areas, like western North America and parts of Europe and Asia, they constitute the major part of the forests, sometimes forming extensive stands of a single species, as in parts of the redwood belt of northern California and the Douglas fir forests of Oregon and Washington.

The earliest fossils referable to the Coniferales have been reported from Permian, or possibly late Carboniferous rocks,[14] but these primitive conifers, some of which also occur in the Triassic, are not certainly referable to any existing families, although suggesting some relationship with them. They seem to have been generalized types, in this respect recalling the Cordaitales. Among these ancient conifers may be mentioned two, Walchia and Voltzia, both of which show a possible relationship with the Araucariaceae, a family now restricted to the Southern Hemisphere. Of the two living genera, Araucaria has representatives in South America and Australasia, the most familiar species, the Norfolk Island pine, *A. excelsa,* being often cultivated. Agathis has a small number of species in Australasia and the Malayan region. The Kauri pine of New Zealand is the best known.

While remains of conifers are abundant from the Permian onward, the earlier fossils are mostly impressions of twigs and leaves, insufficient data for the determination of near relationships.

There is some evidence that conifers really related to the Auracariaceae did exist in the Permian and Triassic, and from the Jurassic onward the family was certainly established and wide-spread.

Some of the early conifers were trees of great size. In the famous Petrified Forest of Arizona, of Triassic

[14] Seward, *loc. cit.*, pp. 279–281.

Age, there are entire trunks of enormous trees, almost rivaling in size the Californian redwoods. These trunks are so perfectly preserved that the wood-structure can be clearly made out. It is said to be practically identical with that of the living species of Araucaria and Agathis. Unfortunately, nothing is known of the foliage and fructifications of these giant trees.[15]

At the present day there is a marked difference between the conifers of the Northern and Southern Hemispheres, most of the genera, and even families, being restricted to one or the other. Thus the pine family, Pinaceae or Abietineae, comprising the pines, firs, spruces, etc., is exclusively northern, and this is true of the Sequoias, bald cypresses and yews, while the Araucariaceae are entirely southern, and the Podocarpaceae predominantly so, although several species occur north of the equator, both in America and Asia. The family Callitricaceae, except for a single species, *Callitris quadrivalvis* of North Africa, is also confined to the Southern Hemisphere.

It is noteworthy that the oldest conifers show indications of possible relationships with the Araucariaceae and perhaps with the Podocarpaceae, both characteristic austral types. This suggests that they are older than the Pinaceae and Cupressineae, which possibly may have been derived from them and isolated in the north, where perhaps the development of a continental climate with its extremes of temperature may have influenced the evolution of these forms, while the more primitive Araucarian and Podocarpus types persisted in the less extreme climate of the Southern Hemisphere.

In the Jurassic, although there are abundant remains of conifers, and many examples of leaves and branches resemble closely those of living genera, the association of these with fructifications that can satisfactorily be assigned to living types is very rare. "Our knowledge

[15] Seward, *loc. cit.*, p. 305.

of Mesozoic conifers is lamentably incomplete; there are many genera and species represented by pieces of sterile foliage shoots, some bearing long and narrow leaves in two ranks, as in the yew and redwood tree (*Sequoia sempervirens*) and several others; some with crowded and more or less sickle-shaped leaves like those of *Araucaria excelsa* or Cryptomeria. It is seldom that the fossil twigs bear cones or other reproductive organs well enough preserved to be used as tests of affinity.'"[16] There is, however, good reason to believe that some of them were really related to living Araucariaceae, as both foliage and cones show a marked similarity to some of the living species of Araucaria.[17]

There is strong evidence that the giant Sequoias, now confined to California, were represented in the Jurassic by closely related species, to which the name *Sequoites* has been given. Later in the Cretaceous, and especially during the Tertiary, Sequoias, identical with, or closely related to the Californian redwood, were wide-spread through the Northern Hemisphere.

In spite of the difficulty of identifying the Jurassic conifers, it is probable that all the existing families were represented—or at least the direct ancestors of these.

During the Cretaceous and Tertiary certain forms, like the Sequoias and the cypress (Taxodium) of North America, Glyptostrobus of Eastern Asia, and other forms of restricted range were abundant and during the mid-Tertiary were wide-spread through the Northern Hemisphere. Later they were replaced by pines, firs, etc., the predominant coniferous trees of the present time.

A small order of gymnosperms, the Gnetales, comprising three very diverse genera—Ephedra, Gnetum and Welwitschia—is quite unknown in a fossil condition, and their relationships are very uncertain. They are sometimes assumed to be intermediate between the other Gymnosperms, and the flowering plants, angiosperms,

[16] Seward, *loc. cit.*, p. 364.

[17] *Ibid.*, p. 363.

but this is far from being proved. Zimmermann[18] believes the order is a very old one, the few living forms being relicts of a very old group.

The Cretaceous, the last period of the Mesozoic, marks a great change in the vegetation of the world. Up to this time, to judge from the fossil record, the vegetation was made up largely of pteridophytes and gymnosperms. Suddenly, apparently—but doubtless this is more apparent than real—the plants show a decidedly modern character. The cycads and Ginkgoales and the Araucarian conifers give place to conifers of a more modern type, cypresses, redwoods, pines and firs, replacing to a great extent the archaic types of the Jurassic. "Considering the conifers as a whole the facts which stand out most clearly are: the greater variety in genera and species in the Cretaceous than in the present northern (European) forests, and the wide distribution in the North Temperate and Arctic of types which have long been strangers in the Northern Hemisphere."[19]

For the first time in the history of the earth's vegetation, the modern flowering plants, the angiosperms, begin to play a leading part. From the lower Cretaceous onward, they increase rapidly in numbers and importance, and soon dominate the floras of the whole world. The early history of these plants is still a mystery. Even in the oldest Cretaceous formations, where remains of angiosperms occur, they are essentially similar to forms existing to-day, and generally the lower Cretaceous angiosperms can be assigned to families, or even genera now living.

It is evident there must have been a long series of antecedent forms, presumably extending far back in geologic time, and there has naturally been much speculation as to what forms, if any, among the Paleozoic and early Mesozoic fossils, may represent the ancestors of the Cretaceous angiosperms. Some look upon the Jurassic

[18] *Loc. cit.*, p. 310.

[19] Seward, *loc. cit.*, p. 397.

and early Cretaceous cycadeoids, as forerunners of the modern angiosperms; others are inclined to look for their descent, directly from fern-like ancestors, possibly as far back as the Paleozoic.

While it is practically certain that true angiosperms existed during the Jurassic, and a few imperfect leaf impressions have been assigned to them, these throw very little light upon the subject. Seward[20] concludes "It is probable that the almost complete absence of fossil angiospermous leaves in Jurassic and older Mesozoic rocks is due, not to lack of flowering plants in the world but their failure to be preserved as fossils because they occupied a tract of country remote from localities where conditions were favorable for fossilization." It might be added that many of them may have been herbaceous plants whose tissues would be preserved only under especially favorable conditions.

The recent discovery of a remarkable group of Jurassic plants, Caytoniales, is of great importance, as these plants, although very different from any existing flowering plants, nevertheless have seeds borne in a closed receptacle that might be called a carpel, and there was a structure suggesting a stigma. The Caytoniales may therefore be called angiosperms, but whether or not they were related to any existing flowering plants is another question.[21]

While all the living angiosperms, sometimes called "anthophytes," are sufficiently alike in their reproductive characters to indicate real relationships, they must represent the result of evolution along many independent lines which originated at a very remote period—perhaps as far back as the Jurassic. Their still more remote ancestors were presumably of the fern-type, perhaps some form of pteridosperms, or possibly derived from

[20] Seward, *loc. cit.*, p. 366.

[21] H. H. Thomas, "The Caytoniales, a New Group of Angiospermous Plants from the Jurassic Rocks of Yorkshire." *Phil. Trans. R. Soc.*, 213: 1925.

true fern-ancestors, like the Ophioglossaceae. The microsporangia (pollen sacs) of most angiosperms are more like the "synangia" of the Eusporangiate ferns, or even the sporangia of Equisetum, than like the microsporangia of the pteridosperms or Cycadeoideae. Attention has been called to the similarity in the development of the young sporophyte in many monocotyledons and ferns, and especially Isoetes. It may be these indicate a real, if extremely remote relationship.

The primary division of the angiosperms into monocotyledons and dicotyledons is a somewhat artificial one, and the theory recently advanced by Engler[22] as to their relationships is probably as plausible as any that have been proposed.

Engler predicates the existence, perhaps in the Jurassic, of a wide-spread development of "Protangiosperms," having most of the essential characters of the existing flowering plants. From this great complex of forms, many lines of true angiosperms developed, some monocotyledons, others dicotyledons; but he believes that neither of these gave rise to the other, and also thinks that none of the existing major divisions of the flowering plants has been derived from any of the others.

From the Cretaceous onward the development of the angiosperms has been very rapid, with a corresponding reduction in the importance of the gymnosperms. This advance has, no doubt, been greatly accelerated by the intimate association of flowering plants and insects—the two divisions of their respective sub-kingdoms now dominating the organic world.

[22] A. Engler, "Die natürlichen Pflanzenfamilien," 2nd ed., Vol. 14a, 1926.

A DOMINANT MUTATION OF FREQUENT RECURRENCE IN SORGHUM

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IT is generally agreed that recessive mutations occur much more frequently than dominant ones; that most recessives are unfavorable rather than favorable in their effect, and that they represent a deleterious rather than an improved condition of an organism or species. The evidence is abundant, showing that recessive mutations occur frequently in nature or may be readily induced through treatment with x-rays.

Especial interest is attached to dominant mutations for the reason that conspicuous gene changes in this direction are infrequently found among the natural mutations and are also rather rare among the mutations induced by irradiation. The types of recessive mutations found most frequently in nature are also the ones recurring the most frequently following irradiation. This appears to be true in Drosophila and in various plant species. Patterson and Muller (1930), in reporting on progressive mutations, conclude that the so-called progressive mutations can probably be produced by artificial irradiation in cases where there is the possibility of their occurring at all. They demonstrated that mutations can be produced by irradiation in both of two opposite directions at the same locus, and true reverse mutations of the forked gene were produced. As a result of irradiation, Stadler (1931) found no clear case of dominant mutation in irradiated plants, but hundreds of typical recessive mutations were produced, many of which were indistinguishable from characters previously found in nature. Dominant mutations of known and recent origin are rare, even in maize, in which more genetic characters have been

studied than any other plant species. A case of a spontaneous dominant mutation, the ragged character, in maize is described by Brink and Senn (1931). Teopod, a dominant character in maize, is another of the relatively few such mutations in corn which, according to Lindstrom (1925), is of recent orgin. While both of these characters have come about through gene mutations from recessive to dominant, neither represents an improvement in the species, but rather, in effect, they are similar to many of the deleterious recessive mutations. Horlacher and Killough (1932) report a mutation induced by irradiation from a virescent yellow recessive to a dominant normal green chlorophyll condition in cotton.

It is the purpose of this paper to describe the persistent and frequent occurrence of a dominant mutation in sorghum involving apparently only a single gene—one that has been appearing regularly during each season that the stock has been grown for the past fifteen years, and to show the rate of this mutation.

The parental stock of sorghum in which this mutation has been recurring came from a crib-run population of 652 heads of Standard Blackhull kafir grown near Chillicothe, Texas, in 1916. Eight lots of ten heads each were selected from this population for certain head characters and planted in head rows in 1917. These eighty heads formed the basis of eight pure lines of kafir, which have been inbred continuously for the past fifteen years and grown in field plats, comprising a total of approximately 3,000 plants each year. Fortunately, evidence is at hand to show that this same mutation was appearing in this stock at least as early as 1916. One of the original heads, No. 500, selected for short rachis, produced a progeny of ten tall plants, averaging 212 cm high, and four plants, normal in height, averaging 159 cm tall, which was quite close to a 3:1 ratio, considering the small population of only 14 plants. Two heads selected from these tall plants were grown the following year, 1918, and bred true for tall. Notes taken that season state that "several ab-

normal tall plants also appeared in the inbreeding plats which seem to indicate that the lines are not yet pure for height''; however, aside from these few plants, all the others appeared normal for height. Our recollection is that these abnormal plants continued to appear each year, more some years than others, but from one or two to five or six occurring each year among approximately 3,000 progeny from the eighty selfed heads. They constituted a source of annoyance, as the lines became homozygous for various characters under study and, with these exceptions, were remarkably uniform. It was felt that perhaps our technique in selfing was at fault and that we were getting some contamination from crossing between the various lines. In spite of precautions of bagging early and carefully the tall plants continued to appear, and since the purpose of this study with sorghums had other objectives, no attempt was made to account for these abnormalities until 1927.

Breeding Behavior of Tall Plants

Each year a few typical kafir plants of unusual height, considerably taller than any other forms or varieties of kafir in cultivation, continued to appear among the normal plants of the inbred lines. The tall plants are typical of the parental pure lines in which they may appear in all characteristics except height, in which respect they are from 75 to 100 cm taller than the normal plants. There appears to be no increase in the number of nodes, and the increased height is due entirely to the elongation of the internodes.

Table 1 shows the height of the tall mutations, the height of the parental line in which they arose, and the height frequency and segregation of the F_2 progeny of certain of the tall mutations grown.

Four of these abnormalities occurred in the inbred lines in 1927, two of which were planted in head-rows the following year. One of these rows segregated 36 tall to 12 normal plants, a 3:1 ratio, while the other gave 59

TABLE 1

HEIGHT OF PARENTS, TALL MUTATIONS, AND THE HEIGHT FREQUENCY AND SEGREGATION OF PROGENY OF THE MUTANTS

Line No.	Height, cm.		Height of progeny. Class centers, cm.																				Total	Segregation
	Mutation	Parent line	125	135	145	155	165	175	185	195	205	215	225	235	245	255	265	275	285	295	305	315		
.....	.....	189				2	3	0	1	2	4					2	3	8	6	6	9	2	48	3:1
1	273	208				3	2	1			3	3	3	5	0	1	0	0	1				22	2.6:1
40	257	180				4	2			1	0	3	1	2	3	4							20	2.3:1
567	279	188			1	1	1				1	3	2	6	5								20	5.6:1
567	267	188				3	1	1			3	4	1	8	2								23	3.6:1
223–3	214	162		3	4	4			1	7	11	6	1										37	2.3:1
654–6	224	161	2	4	3	1		1	8	7	4	4	2										36	2.6:1
F_3 progenies from 3 normal F_2 plants					4	7	11	7															29	Homo.
					2	14	11	8															35	Homo.
					6	4	11	8															29	Homo.
F_3 progenies from 5 tall F_2 plants											1	4	5	7	8	10	3						38	Homo.
					2	0	3	4			4	5	2	6	6	5	1						38	3.2:1
					2	0	5	2			4	2	3	6	3	2	2						31	2.4:1
					12	6				2	14	16	7	2	1								60	2.3:1
				2	4	1	1	2			2	8	3	9	4	1							37	2.7:1
F_4 means of last F_3 progeny above				5	5			6	6	9	6												37	1:2:1

tall and 27 normal plants, or a ratio of 2.19:1. Heads from three of the normal recessives and five of the dominant tall plants were grown in 1929. All the recessives bred true for normal height. One of the tall plants bred true for tallness and the other four segregated tall and

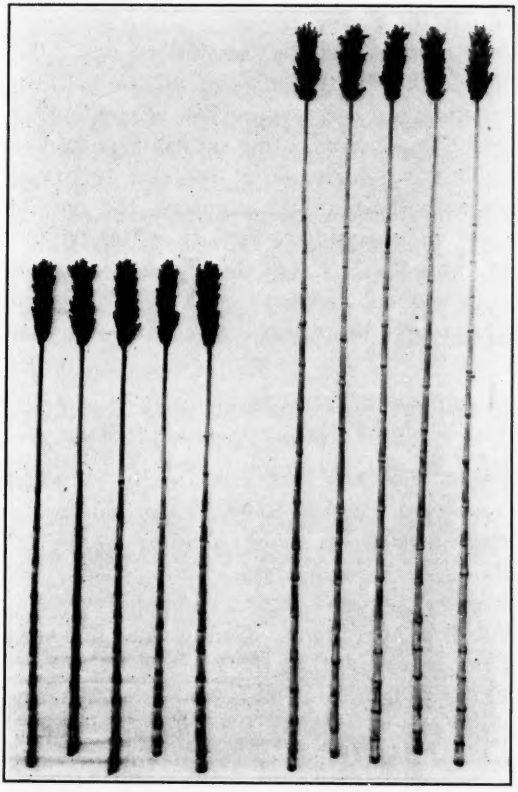

FIG. 1. Normal kafir (left) and the tall type resulting from a single dominant gene mutation (right).

normal in ratios approximating 3:1. The entire population of 37 plants from one of the latter heterozygous rows was grown into the next generation. The progeny from the ten recessives were all normal in height. From

the 27 tall plants 16 progenies segregated tall and normal and 11 bred true for the tall type. Thus the breeding behavior of these 37 plants approximated the 1:2:1 ratio expected when only a single factor difference is involved.

Four more tall mutations appeared in the plats in 1928 and these, together with two of those occurring in 1929, were tested in the F_2 generation. All segregates fell into one of two distinct classes, normal or tall. The total population in the F_2 progenies of all the tall mutations tested during these three years has been 1,740, of which 1,310 were of the dominant mutant tall type and 430 were normal. This is a deviation of only 5 ± 12.2 from a 3:1 ratio, and with the numbers involved, the possibility of the segregation belonging to any other Mendelian ratio is virtually eliminated. From the F_2 generation both the homozygous normal recessive and the homozygous tall mutant types have been perpetuated and found to breed true.

TESTS FOR EFFECT OF CROSSING UPON FREQUENCY OF TALL TYPES

In view of the fact that crossing in sorghums frequently results in marked hybrid vigor, the cross showing marked increase in height similar to the tall type plants discussed herein, it might be suspected that this new type arose through hybridization and was merely the expression of hybrid vigor. Conner and Karper (1927) have shown, however, that the marked hybrid vigor, as measured by height of plant, which accompanies the crossing of widely related sorghums, is absent when closely related forms, such as two strains or varieties of kafir, are crossed. Several of the pure lines of kafir, among which these tall mutations have been recurring, have been previously crossed also, and unpublished data on height and other measurements show a lack of observable hybrid vigor accompanying such crossing. Even though sorghums cross-pollinate readily (Karper and Conner, 1919), the eight pure lines of kafir grown in this

block of sorghums each year are fairly well isolated from other sorghums, and all the plants were carefully self-fertilized by bagging the heads before exsertion from the boot began. Under these conditions it was difficult to see how cross-fertilization could account for the regular and frequent recurrence of the abnormal tall plants.

Furthermore, the mutants are much taller—75 to 100 cm—than any normal kafir plants, and if it was assumed that they arose from seed which in some way became crossed with one of the other pure lines and, therefore, were F_1 hybrids, this would explain their presence and origin only if a hybrid had been accomplished between two of the lines which bore complementary height factors. In such event the F_2 generation would segregate in some form of a 9:3:3:1 ratio if only two height factors were involved. As has previously been shown, however (Table 1), the F_2 segregation is simple, involving only a single gene for height.

In 1928 one of the dominant tall mutations appeared among the normal plants in each, Line No. 1 and in Line No. 40, and two of them in Line 567. In order to further eliminate the possible theory that these abnormal plants might be due to cross-fertilization, each of these three lines was intercrossed with each of the other seven pure lines of kafir in the inbreeding blocks in 1929. Eighteen combinations of crosses included all the possibilities. Pollen from one of the parental lines was dusted over the flowers of another on successive mornings as they bloomed, with the expectation of identifying the hybrids on the basis of hybrid vigor in the first generation. Previous experience with this method of crossing sorghums has shown that a considerable number of F_1 hybrids can be recovered by trimming off all the seed branches not flowering on the mornings when dusted with pollen from the plant used as the male and planting the remaining seed of the female plant the next season and identifying the F_1 hybrids through hybrid vigor, seed color, red stem or some other known character. The per-

centage of hybrids will vary with varieties used but will ordinarily be more than 10 per cent., a cross-pollination of Freeds x milo, for example, resulting in 40 per cent. F_1 hybrids appearing among the progeny the next season.

If the tall type plants are true mutations and not due to hybridization, they should occur only as frequently when the lines are intercrossed as among the inbred lines. If, on the other hand, the tall plants were the result of hybridization and the bringing together of complementary factors in the crossing process, their number should be markedly increased in the progeny of such intercrossed lines. Of course, some of the actual crossed seed would be expected to produce the tall mutant type plants, even though tallness is not due to crossing, as the result of pollen carrying the mutated gene fertilizing a normal ovule, or *vice versa*.

A population of 120 plants was grown in 1930 from each of the female parents which had been subjected to pollen from companion lines in making the eighteen combinations of crosses, and a total of four of the abnormal tall plants were present among the total progeny population of 2,160. One tall plant occurred among the progeny of the cross of Lines 40 x 223, one in Line 567 x 654 and two in Line 1 x 223. None was present in any of the other crosses. It happens that the female parents of those three crosses in which the tall plants appeared were the same as those in which the tall mutations appeared in 1928 when the parents were grown from selfed seed. There were four of the tall plants in the total population of 990 in these three lines in 1928 and the same number in a total population of 360 plants where the mother parent had been dusted with foreign pollen. The percentage of tall plants is higher than was found in the inbreeding plats but not sufficiently high to warrant the conclusion that they were due to crossing. If cross-pollination were responsible, the number of tall plants should have been increased approximately 25 times and should have con-

stituted at least 10 per cent. of the total population. Lines No. 223 and No. 654, in which mutations have previously occurred, and Line No. 153, in which they occurred later, produced no tall plants among the progeny when subjected to pollination with pollen from the other pure lines; however, a considerable number of the progeny must have been crosses, detection of which was not possible in the F_1 because of the close relationship of the parents and the lack of hybrid vigor.

These four abnormal tall plants were grown in 1931 and all segregated for height into tall and normal plants, the average ratio being 3.4:1. Head type and other visible characters in these progeny resembled the mother stock from which these abnormal tall mutations came, except in one instance—the progeny of the tall plant arising in the population from the mother head in Line 567 that had been subjected to pollination with Line 654. In this case the characters of the pollen parent were unmistakably evident in the F_2 progeny. Line 654 is characterized by few seed branches, few nodes and other distinguishable characters, while Line 567 carries a higher number of both seed branches and nodes. Compared with the F_2 progeny of a tall mutation arising directly from the inbred Line 654, which averaged 29 seed branches and 3 nodes, the F_2 progeny of the tall mutation appearing in Line 654, when subjected to pollen from Line 567, averaged 43 seed branches and 4 nodes, intermediate between the two parents, and was segregating for these characters. Line 567 averaged 57 seed branches and 6.6 nodes to the head. It is evident, therefore, that this particular tall mutation was an actual cross between Lines 567 and 654 and that either the pollen from Line 654, or the ovule in Line 567, carried the dominant mutant gene which met with a normal one, producing a heterozygous tall plant. According to the rate of mutation in the inbred lines, this would be expected to happen about one time in 605.

EFFECT OF THE MUTANT GENE ON OTHER PLANT CHARACTERS

Mutations appearing within a given pure line seem to be identical with the parent line in all observable characters except height of plant. Opportunity to definitely establish this fact was afforded in 1929 when mutations appeared in Lines No. 223 and No. 654, two inbred lines having many widely contrasting characters. Line No. 223 is characterized by having a long head, long rachis, short seed branches and many nodes in the head, while Line 654 has a shorter head, short rachis, long seed branches and few nodes in the head. These quantitative characters are quite sharply contrasted in the two lines. Crosses had previously been made between these two lines for a study of the inheritance of these quantitative characters. Although the data have not yet been published, the progenies were carried through the F_3 generation and show number of seed branches, number of nodes in the head, length of rachis and length of seed branches to be characters inherited in a simple Mendelian fashion.

Typical abnormal tall plants occurred in each of these two lines in 1929, and the difference existing between the various characters of these two mutant plants in these contrasted lines can be seen and compared with the means of normal plants of these same parental lines (Table 2). The table also affords a comparison of these characters in the F_2 generation and in the normal plants of the parental lines. The head and plant characteristics of these two mutations are very much like those of the respective parental lines from which they arose, except in height. In Line 223 the mutation had a long head, long rachis, long seed branches, many seed branches and many nodes in the head, while the mutation in Line 654 had the opposite characteristics. Further evidence of the stability of these same characters in the mutations, exactly in keeping with their expression in the pure lines

TABLE 2

COMPARISON OF CHARACTERS IN MUTATIONS, TALL SEGREGATES, AND NORMAL PLANTS FROM SAME INBRED LINES

Material	No.	Height of plant	Length of head	Length of rachis	Length of seed branches	No. of seed branches	Nodes per head	Nodes per plant
Tall mutant in Line 223 (1929)	1	214	25	20	6.1	67	8	.....
Tall segregates in progeny (1930)	26	204.12 ± 1.19	23.23 ± .30	16.04 ± .40	6.46 ± .11	62.62 ± .75	7.08 ± .19	14.96 ± .09
Kafir, Line 223 (1930)	11	122.68 ± 2.09	21.45 ± .56	16.77 ± .31	6.18 ± .12	54.82 ± 1.25	5.27 ± .09	14.18 ± .15
Difference		81.44 ± 2.41	1.78 ± .64	.73 ± .51	.28 ± .16	7.80 ± 1.46	1.81 ± .21	.78 ± .17
Tall mutant in Line 654 (1929)	1	224	23	12	7.5	44	5	.....
Tall segregates in progeny (1930)	26	197.58 ± 1.79	21.62 ± .36	10.65 ± .31	9.35 ± .30	30.12 ± 1.19	3.38 ± .10	14.73 ± .11
Kafir, Line 654 (1930)	12	137.83 ± 1.84	21.17 ± .49	9.50 ± .59	8.58 ± .33	26.33 ± 1.65	3.58 ± .19	13.50 ± .10
Difference		59.75 ± 2.57	.45 ± .61	1.15 ± .67	.77 ± .45	3.79 ± 2.03	.20 ± .21	1.23 ± .15

themselves, is found in a comparison of the means of the tall segregates in the F_2 generation of the mutant types and the parental lines grown the same year. The difference between height of plant in the two populations is, of course, highly significant, but all the other characters in the tall progeny are the same as in the parental lines, except number of nodes in the head and in the plant. In nodes per head the difference is more than three times the probable error in Line 223, but there was no significant difference in this character in Line 654. Number of nodes per plant shows a difference significant in relation to its probable error in both lines. The largest difference is in Line 654 and is undoubtedly due to the small number in the population of the parental line and failure to get a random sample of measurement of this character. Further, the relative constancy of number of nodes per plant results in a low standard deviation of the mean, a low probable error, tending to exaggerate the significance of a small difference. Actual average number of nodes common to this line over the past five years was 14.9, or more than one node above the mean obtained from the sample used in this table, so that the significant difference between the population with respect to this character is more apparent than real.

Means of the F_2 progenies were calculated separately for the normal and tall segregates and show a very close similarity of both classes for all characters except height of plant, the only one differing significantly. Thus the tall plants are recovered in the F_2 generation identical with the original mutation and having all the attributes of the parental line from which it arose except height of plant, for which apparently only a single gene is responsible.

RATE OF MUTATION

Before trying to analyze the data so as to arrive at conclusions regarding the rate of mutation, several important points should be disposed of. The eight pure lines

of sorghum, each with a population of 330 plants grown every year, comprised a total population of 2,904 inbred plants annually, and tall mutations have occurred in six of these eight lines in the past four years (Table 3). In-

TABLE 3

RATE OF DOMINANT TALL MUTATIONS WITHIN EIGHT PURE LINES OF SORGHUMS, 1927–31

Year	Line No.	No. of mutations	Total population	Mutation ratio	
				Zygotes	Gametes
1927	All	4	2,904	1: 725	1: 1451
1928	1	1	330	1: 329	1: 659
1928	40	1	330	1: 329	1: 659
1928	567	2	330	1: 164	1: 329
1928	Composite	1	264	1: 263	1: 527
1928	All	5	2,904	1: 580	1: 1161
1929	1	1	330	1: 329	1: 659
1929	223	2	330	1: 164	1: 329
1929	654	1	330	1: 329	1: 659
1929	All	4	2,904	1: 725	1: 1451
1930	1	1	330	1: 329	1: 659
1930	Composite	1	264	1: 263	1: 527
1930	All	2	2,904	1: 1451	1: 2903
1931	1	2	330	1: 164	1: 329
1931	153	1	330	1: 329	1: 659
1931	223	2	330	1: 164	1: 329
1931	567	1	330	1: 329	1: 659
1931	654	1	330	1: 329	1: 659
1931	Composite	2	264	1: 131	1: 263
1931	All	9	2,904	1: 322	1: 644
Total	All	24	14,520	1: 604	1: 1209

cluded in this total each year, also, is a population of 264 plants in check plats grown from massed seed of the eight lines. Mutations have been recovered more frequently in some lines than in others, as, for instance, in Line 1 the mutations have appeared every year, whereas, in Lines 192 and 646 none has occurred in the four-year period. In Line 646, however, a tall plant, apparently identical with the mutations found in the other lines, did appear in 1930 among the progeny of 500 seed treated

with x-rays. Whether this same gene mutation was induced by radiation or was already present in the stock before treatment is not known, but the latter would seem the more likely. Only one mutation has appeared in Line 40, while five have been found in Line 1. Is this difference significant and is the mutation rate of Line 1 different from Line 192, in which no tall plants have been found, or can we combine all the lines into one population in considering the rate of mutation?

If we assume that 1:604, the proportion of mutations found in the total population of all eight strains, is the true, or approximately true, rate of mutation, we may consider the probabilities of the various possible proportions of mutations to be represented by the expansion of the binomial $\frac{1}{605}+\frac{604}{605}$. The probability of getting any given number of mutations in a sample of 1,320, the number grown in each line during these four years, may be found by expanding $(\frac{1}{605}+\frac{604}{605})^{1320}$. By partial expansion of this binomial the probabilities of getting from 0 to 10 mutations in a sample of 1,320 have been computed.

It is found that the probability of getting no mutations in a sample of 1,320 is .11, which is equivalent to odds of 8.1 to 1 against the possibility of getting no mutations in the population of 1,320 plants, the number involved in Lines 192 or 646, respectively.

The probability of getting 5 mutations in a sample of 1,320, assuming 1:604 as the true rate of mutation, is .05, representing odds of 19 to 1 against such occurrence due to chance. The probability of getting 5 or more mutations in a sample of 1,320 is .07, representing odds of only 13.3 to 1 against such occurrence. Apparently Lines 1, 40 and 192, in which five, one and no mutations, respectively, have occurred, need not be considered as differing significantly in rate of mutation.

In each of the five years the total number of plants grown from the eight lines was 2,904, but the number of mutations observed in this population varied from two to

nine. Is this a seasonal difference or is it a chance fluctuation? By the expansion of the binomial used above to the power 2,904 we find that the probability of getting two mutations, the smallest number obtained in any one year, is .10, which is equivalent to odds of only 10 to 1 against such occurrence, while the probability of getting two or less is .14, representing odds of 6.1 to 1 against such an occurrence in a sample of 2,904. The probability of getting nine mutations in a sample of this size is .03, representing odds of 32.3 to 1 against such occurrence; however, the probability of getting nine or more mutations in such sample is .05, representing odds of only 19 to 1 against such occurrence due to chance.

It is seen from these probabilities that the distributions discussed above are all within the limits of chance variation, if the rate of mutation is 1: 604, and it appears that grouping all lines and all years into one population is justified.

The total combined population of the eight inbred lines grown during the past five years was 14,520 plants, and a total of 24 tall mutations appeared during this period (Table 3). The mutation ratio, considered on the basis of zygotes, is 1 to 604. Presuming that the mutation of this gene may occur as readily among the male gametes as among the female gametes, the mutation ratio in the gametes is 1 to 1,209, or 827 per million.

Discussion

Since this tall character is clearly a dominant, it could not be carried along as a latent character, and its recurrence is undoubtedly the result of frequent gene mutation. The mutation likely occurs during gametogenesis of the parental plant, the generation prior to the appearance of the tall plants, where a gamete carrying the mutated gene unites with a normal gamete and produces the seed from which the heterozygous mutant plant develops. A normal ovule fertilized by pollen carrying the mutant gene, or an ovule carrying the mutation fer-

tilized by normal pollen, would explain the hybrid condition and simple segregation in the progeny of the tall plants.

It is quite improbable that the abnormal tall type plants are the result of abnormal chromosome behavior because of the simple hereditary performance of their progeny. If a chromosomal aberration is responsible, and a whole section of a chromosome rather than a single gene is involved, then the factors for number and length of seed branches, length of rachis and number of nodes in the head must be located on another chromosome than the one involved with the tall type, because these characters appear to segregate normally in the progeny of the mutant type plants.

If the tall plants were the result of a bud mutation occurring in a somatic cell somewhere in the ontogeny of the plant, except tissue just previous to that concerned in pollen mother cell development, a certain area of considerable size should sometimes be affected and instead of one seed, or a very few seed, on the head producing a tall plant, a considerable number of such plants should result. Furthermore, such an area on the panicle, resulting from the outgrowth of a somatic cell in which the gene had mutated from normal to tall, would be heterozygous, producing two kinds of gametes, *T* and *t*, and one out of four of the seed set should produce a *TT* plant that would breed true for tall. The new tall type is dominant, segregates clearly from the normal, and one third of them breed true. All the tall mutations tested have segregated 3:1 in the succeeding generation. Of course, there is still the possibility that a somatic mutation occurred just previous to reduction division but so late in development that it affected only the pollen mother cells or the megaspore mother cells but not both. The results of such a somatic mutation would be substantially the same as one occurring during reduction division, except that a mutation just previous to reduction division might be expected to cause a number of the mutants to

appear within the progeny of a single family. It is true that on four occasions there have been as many as two mutants among the progeny of a single line, while other lines showed none. The probability of finding two or more mutants in a population of 330 plants, from material mutating at the rate of 1:604, is .10 and would be expected to occur once in ten trials. However, two mutants appearing in a single line actually occurred four times out of twelve trials, which is rather frequent on the basis of the probabilities involved. If the two mutants observed in each of these instances were considered as the result of only a single mutation the total number in the four years would be reduced from 24 to 20 and the rate of mutation would be 1:726 zygotes instead of 1:604, the rate when each mutant plant is regarded as a separate mutation.

It appears quite certain that we are dealing here with a single dominant gene which increases the height of the plant approximately 40 per cent., increases the production of the plant, and can be definitely classed as a favorable mutation in the biological sense. Economically, this new type is superior from the standpoint of forage and silage and is being tested and distributed for this purpose. From the standpoint of convenience in harvesting for grain, however, it would be considered inferior to the parental types, as pointed out later.

Not only is this gene change a dominant and favorable one, but there is evidence that the mutation has been recurring under natural field conditions, at least during the past 15 years, and the rate of mutation during the past four years has been very high when compared with the mutation rate of genes studied in other species. Stadler (1931), in studying the frequency of recessive mutations in eight well-known genes in maize, found the most mutable gene yielded about 400 mutations per million gametes. In this gene for height of plant in sorghum, the rate of mutation was 827 per million gametes, or about twice as great as the most mutable

gene among the recessives studied in maize. Although the specific dominant tall gene in sorghum is highly mutable, a number of recessive gene mutations have been found much less frequently in these same inbred lines of kafir (Karper and Conner, 1931). During the past 15 years two recessive gene mutations affecting chlorophyll development have occurred in each of three of the inbred lines, while none has appeared in the other five inbred lines. While accurate data on the rate of mutation for any one of the specific chlorophyll deficient genes are lacking, the rate of these more or less common recessive mutations is certainly very low, when compared with the frequent recurrence of the dominant mutation discussed in this paper.

In the sorghums we find what appears to be a parallel series of height variations common to a number of the subspecies or varieties. For example, in each of the kafir, milo, feterita, kaoliang and broomcorn groups we have strains or varieties known as Standard, Dwarf and Extra Dwarf. The original introduction of these subspecies of sorghum was practically all the Standard or taller types, and the Dwarfs and Extra Dwarfs originated, for the most part, by mutation in this country during the past two or three decades and have very largely replaced the tall or Standard types originally imported from Africa, largely because of the convenience in harvesting and not because they are more productive. Data on the inheritance of height in this series of plant statures indicate that a single factor is responsible for height difference between Standard and Dwarf and another factor responsible for the difference between the Dwarf and Extra Dwarf series. These single genes responsible for height differences in sorghum are illustrative of the vast economic potentialities that may be packed in a single recessive gene. Prior to 1906, all the milo grown in the United States was of the tall or Standard variety. About that time Dwarf milo suddenly

appeared, undoubtedly through a natural recessive mutation of a single gene. Its desirable characteristic was recognized, the seed supply increased, and the new type soon replaced practically all the Standard variety. To-day, at least 50 million bushels of grain, annually, are grown from Dwarf milo, a simple recessive from Standard milo and differing only in height of plant, which has certain advantages in harvesting as a grain crop.

The tall mutation described here is in the direction of increased height and a dominant representing a stature above the common Standard kafir but differing from it only by a single gene. Although this new mutant type is not common to the sorghums in this country, the foreign introductions, which have undergone little selection, are generally tall-growing types, so that this tall mutant type is probably present among the native sorghums in Africa and India, and the specific gene mutation described here may be a reversion to the wild type.

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NOTES ON FEEDING AND MOLTING IN FROGS[1]

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INTRODUCTION

FOR a number of years the writer has been working, by the customary dissection method, on the food of frogs of the eastern United States. Supplementary and somewhat preliminary to this, a few experiments have been conducted in hopes that a better understanding of the food of frogs might be obtained.

FEEDING

Experiments on the feeding of frogs are not numerous, although much dissection work has been done to determine stomach contents. One of the most complete records of the diet of an individual frog appears in D. C. Beard's "American Boy's Handy Book." He itemizes the daily diet of a frog, probably *Rana catesbeiana,* from May 14 to November 17. During this period, the frog consumed 12 beetles, 9 mice, 1 frog, 3 crawfish, 1 bat, two thirds of a perch, and, in addition, tackled a young alligator 11¾ inches long. The latter was disgorged by force. Miller (1909) observed that a toad took ninety to one hundred rose beetles at a single feeding. In the report of the Porto Rico Experiment Station (1926) we learn that a Surinam toad will eat nearly 10,000 injurious insects in three months.

Robert Matheson, a twelve-year-old boy of Ithaca, N. Y., amused himself and friends one evening by feeding fireflies (Lampyridae) to a frog. The fireflies emitted their cold light through the thin skin of the cold-blooded animal.

[1] Read before the American Society of Zoologists at New Orleans, December 30, 1931.

Feeding experiments were conducted in the following manner. Individual frogs were placed in battery jars with about an inch of clear water in the bottom. The tops of the jars were covered with cheesecloth to prevent undesirable insects from entering. Every morning, the ejected pellets and cast skins, when present, were removed and the frogs were transferred to clean jars. At the same time, live food, chiefly spiders and insects, was introduced. The water served to keep the frogs moist and facilitated in securing the molted skins. Records were kept of the food offered to the frogs, the recovery of such food in the feces and dates when molts occurred (see Tables 3 and 6).

It is evident from Table 1 that the frogs were underfed rather than stuffed. If it be true, as some writers state, that a toad will take 10,000 injurious insects in three months, the frogs represented below must have been on a diet.

TABLE 1

QUANTITY OF FOOD TAKEN BY FROGS

Species	Sex	Size	Insects offered	Insects eaten	Insects refused	Duration of experiment
Rana sylvatica	♀	1¼″	182	106	77	Aug. 24–Oct. 21
Rana clamitans	♀	4″	335	286	49	June 12–Oct. 29
Rana clamitans	♀	3½″	65	43	22	Sept. 23–Oct. 28

The maximum amount of food taken by any of the frogs mentioned in Table 1 occurred on October 5, when *Rana clamitans* accepted fifteen insects, then refused to take more. Table 2 gives the menu for this occasion.

Rate of digestion: Concerning digestion, Holmes (1927) states that it is comparatively slow in frogs and the time varies with the amount of food accepted. Langlen (1881) observed that earthworms require somewhat less than twenty-four hours to digest, but if several are given, they do not disappear from the stomach until a longer period.

TABLE 2

MAXIMUM CAPACITY OF *Rana clamitans*[2]

Time food offered	Nature of food	Manner of accepting food
1 P. M.	3 Grasshoppers	Instantly
	1 Xylocopa	"
3:30 P. M.	1 Xylocopa	1 hour later
3:45 P. M.	1 Syrphus fly	Instantly
	1 Spider	"
	1 Moth	"
4:15 P. M.	3 Spiders	Instantly
	1 Fly	"
	1 Bee	"
4:45 P. M.	1 Spider	Instantly
	1 Vespa	Later in evening

[2] This four-inch frog took two flies the preceding day. The following day nine insects were offered, but only seven were accepted.

The duration of the digestive process, or better stated here, the time required for food to traverse the alimentary canal, was determined by feeding insects to a frog and later recovering these insects or parts of them in the excrement. One kind of food, for example, arachnids, was fed for several days, then a beetle or a wasp was offered. These insects could readily be detected in the feces, but much food had to be fed in order to trace a single species. This method of experimentation may have certain disadvantages, for the frog is subjected to unnatural conditions, especially the lack of exercise. A sample record sheet from laboratory notes is given in Table 3. The interception of several insects is shown, especially *Anasa tristis,* the common squash bug, and a Tipulid, which give positive records.

Table 4 is a summary of insects recovered in the feces of three different frogs, two *Rana clamitans* and one *Rana sylvatica.* The species showed little difference in the rate food passed through the alimentary canal. It is apparent that the stomach must be emptied on the average of once in two or three days. The rate is more

TABLE 3

A PART OF THE RECORD OF *Rana clamitans*. ♀, 4 INCHES LONG

Date	Insects offered	Parts of insects recovered in defecations		
		Heads	Thoraces	Wings
June 29	5 Muscids 1 Tenebrionid 1 Honeybee (*1 Anasa*)	3 Hymenoptera	2 Sphecius	3 Hymenoptera
30	12 Muscids	3 Hymenoptera	1 Diptera	2 Sphecius 2 Aphids 4 Muscids 1 Hymenoptera
July 1	6 Muscids 1 Noctuid 1 Caterpillar 1 Chalybion 2 Sceliphron	(*1 Anasa*) 2 Diptera 2 Coleoptera	(*1 Anasa*) 2 Tenebrionids	(*4 Anasa*) 9 Muscids 2 Coleoptera 8 Hymenoptera
2	6 Muscids (*1 Tipulid*)	1 Sceliphron 7 Diptera	1 Chalybion	13 Diptera 1 Sceliphron
3	2 Tenebrionids 4 Muscids	7 Muscids 1 Sceliphron	1 Sceliphron	6 Sceliphron 4 Schalybion
4	1 Chalybion 1 Calopteryx	6 Muscids 1 Chalybion (*1 Tipulid*)	(*1 Tipulid*) 1 Sceliphron	2 Sceliphron (*2 Tipulidae*) 5 Muscidae
5	Nothing			1 Chalybion
6	4 Sceliphron 1 Muscid 1 Bombus			
7	1 Honeybee 5 Snails 1 Carabid	1 Chalybion 2 Tenebrionids 1 Muscid	1 Sceliphron 1 Muscid 1 Tenebrionid	Calopteryx 4 Tenebrionids 4 Sceliphron 4 Muscids

rapid if food is abundant and slower if the stomach is not full. When the alimentary canal is crowded with food, digestion is not complete and large parts of insects, often whole insects are voided, but when food is limited, digestion is more complete and insects are frequently digested beyond recognition. Portions of a few insects were voided the same day they were fed, but the majority of the insects did not appear in the feces until one or two days after the frog accepted the food. In one case, parts of a beetle were recovered seventeen days later.

TABLE 4

TIME REQUIRED FOR FOOD TO TRAVERSE THE ALIMENTARY CANAL OF FROGS

Days after feeding to frogs	½	1	2	3	4	5	6	7	8	9	10	17
Number of insects[3] recovered from frogs	3	66	61	43	27	8	8	4	4	3	1	1

Not all food taken into the mouth of frogs passes through the alimentary canal. Gadow and Strickland (1909) relate the interesting habits of an Australian Hyla that vomited the shells of snails taken the preceding day. Undesirable parts of insects are cast aside before swallowing. I have seen frogs break off the tips of the wings of *Calopteryx maculata* and cast them aside. Sticks and stones are sometimes found in the stomach, but they are often discarded before passing the mouth. If a bee or wasp stings, after it is taken into the mouth, the frog quickly rejects it. The sensation may persist after the insect is expelled, but the frog continues to evert its tongue for several minutes as though the insect was still present.

In swallowing, the frog frequently goes through considerable contortions. The head is lowered, the eyes are depressed within their sockets and the frog often uses its feet to adjust or push the food down into the stomach.

Slow-moving objects, as snails, attract the attention of hungry frogs as well as faster insects, for instance, bees and wasps. A quick raising of the head or a right-about turn may indicate that the frog is aware of the presence of food. Their bulging eyes permit them to discern objects almost in back of them.

Feeding continues throughout the summer at a uniform rate except when food is not abundant, when the frog becomes full or possibly slackens during molting. The writer has observed them feeding even in the midst of a molt.

[3] This includes only insects or parts of insects that could be definitely traced.

Molting

Writers of Amphibia mention briefly that molting occurs in transformed frogs periodically at varying intervals, usually about once a month. None except Knauer (1879) give detailed figures on the molting process. He described molting in reptiles and Amphibia and we reproduce herewith the portion dealing with toads.

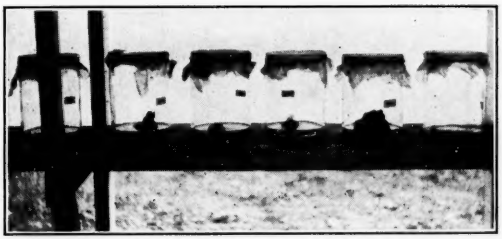

Fig. 1. A series of frogs under observation to determine feeding and molting habits.

TABLE 5

Molting in Amphibia After Knauer 1879

Species	Sex	March	April	May	June	July	Duration
Bufo vulgaris	old ♀	18	19	17	20	18	at most an hour
Bufo vulgaris	old ♀	24	26	23	24	25	at most an hour
Bufo vulgaris	young ♂	22	24	25	24	26	at most an hour
Bufo variabilis	♀		19	21	25	23	brief
Bufo variabilis	♂		24	26	29	30	brief

Fischer-Sigwart (1897) state that *Rana fusca* has monthly molts: the first occurs from late February to early April; the second the latter part of May to the first of June; the third in July and the fourth in August. Wilder (1925) has shown that the mechanism which sets in action the molting process may stimulate a series of molts in rapid succession. Adolph and Collins (1925) believe that a chemical action starts the molting process, while Adams, Richards and Kuder (1930) show that the

thyroid and pituitary glands play a part in the molting of Triturus. Holmes (1927) and Noble (1931) treat of the molting process generally. The writer adds a few original records of the molting habits of four North American species.

Table 6 shows little or no tendency to monthly molts as the general rule in Amphibia. Molts are numerous and frequently prolonged for three or four days. (While the table indicates periods of four-day molts, laboratory notes show that molts frequently started in the afternoon and terminated in the morning, so that molts seldom

FIG. 2. Type of jar for studying feeding and molting.

TABLE 6
MOLTING RECORDS OF FROGS

Species	Sept.	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
Rana clamitans				×		×	×	×				×			×			×						×			×	×		
Rana pipiens		×	×			×	×						×			×		×						×					×	
Rana sylvatica		×	×		×			×	×						×	×								×	×		×	×		
Rana sylvatica																						×	×			×	×			
Bufo americanus					×	×									×	×	×											×	×	

Species	Oct.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Rana clamitans					×	×						×	×			×	×		×	×			×				×	×			×
Rana pipiens			×						×					×							×			×			×			×	
Rana sylvatica					×							×	×			×															
Rana sylvatica				×					×			×		×				×		×			×				×	×	×		
Bufo americanus		×													×	×	×	×												×	×

Species	Nov.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Rana clamitans		×			×				×	×					×					×	×								×	×	
Rana pipiens				×	×						×					×				×							×				
Rana sylvatica																															
Rana sylvatica				×				×						×			×	×								×	×	×			
Bufo americanus		×	×						×	×	×				×	×	×														

Species	Dec.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Rana clamitans								×													×							×	
Rana pipiens						×											×												
Rana sylvatica																													
Rana sylvatica				×	×								×					×	×						×				
Bufo americanus							×	×	×	×													×						

exceeded seventy-two hours.) Resting periods between molts are not clear-cut, except in the case of *Bufo americanus*. In the toad, there is a tendency towards molts twice a month, with distinct resting periods between and molts extending over three or four days. When cold weather approaches, the molting process slackens. During November and December, the frogs under observation were kept indoors where the temperature ranged between 40 and 70 degrees F., and we find an interesting prolongation of the molting process almost to the end of December.

Feeding, as noted before, generally ceases during the shedding of the skin, but it is not unusual for a frog to take food during this time, if the skin is not loose about the mouth. It is questionable whether there is a direct correlation between feeding and molting. Frogs under observation molted frequently but were at no time overfed. Molting also occurred in *Hyla pickeringii* early in spring before feeding commenced. It is furthermore known that starving newts and other animals molt.

There seems to be some diversity of opinion whether frogs eat their molted skins. Cunningham (1912) and Noble (1931) state that many frogs and salamanders eat their newly shed skin. The writer has observed numerous molts in *Rana sylvatica, Rana clamitans* and *Bufo lentiginosus americanus,* but has never seen these species eat their molted skins. Dissections show that *Hyla pickeringii* often eats its first molt in early spring. A series of thirty-five specimens of *H. pickeringii* were collected at Arendtsville, Pennsylvania, on April 5. They had apparently emerged from their hibernation quarters very recently and probably took trash and their molted skins in the absence, at this time, of more nutritious food. Trematodes, a part of the fauna of the intestine of this species, were found in abundance, sometimes as many as twenty-five in a single frog.

As to the manner of shedding the skin, a variety of opinions exist. Simpson (1913) states that newts shed

TABLE 7

CONTENTS OF THE ALIMENTARY CANAL OF 35 *Hyla pickeringii* COLLECTED APRIL 5, 1923

Contents of alimentary canal	Empty	Insect food	Foreign material	Molted skins	Trematodes
Number of frogs	2	4	9	7	26

their skin in one piece, Wright (1920) believes that the toad and the salamander shed in one piece. The writer is of the opinion that toads and frogs as a rule shed their skin in several pieces.

In closing, it might be well to state that although salamanders, frogs and toads are closely related, their feeding and molting habits apparently differ.

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A CONTRIBUTION TO THE ECOLOGY OF THE SALT MARSH SNAIL, *MELAMPUS BIDENTATUS* SAY

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THE salt marsh snail (*Melampus lineatus* or *bidentatus*, Fig. 1) is a minute species, one of the smallest of our

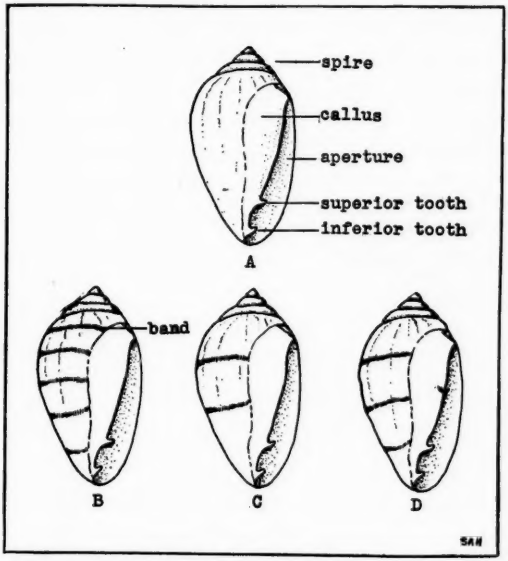

FIG. 1. The salt-marsh snail (*Melampus bidentatus*). A. Typical shell of adult snail, lacking the transverse bands. B, C, and D. Shells of young snails, showing typical variability in banding.

native *Gasteropoda,* being nine to twelve millimeters in length when fully grown. It occurs all along the Atlantic Coast, and is the commonest form in salt marshes and tidal estuaries, being found in both salt and brackish waters, and extending from Massachusetts to Florida and along the shores of the Gulf of Mexico as far as

Texas. It occurs most abundantly in the New England portion of its range.

Very little variation occurs in the shape of the shells in this species, which is ovoid. The much-compressed spire consists of three small whorls; a fourth and largest whorl comprises almost the entire bulk of the shell. The slit-like aperture, narrower at the posterior than at the anterior end, is about three fourths the length of the entire shell.

A considerable latitude, however, is found in the coloration and the banding. The color ranges from a pale yellow through a light brown to a darker brown, to olive brown, sometimes reaching nearly to a black. The transverse bands may be absent in adults, but present, in numbers from one to six or seven, in the young.

The aperture of the shell is bordered by a white, smooth area which is called the callus. Two prominent, whitish ridges which appear like teeth (superior and inferior tooth) when viewed ventrally, are present on the inner wall of the aperture.

The following account of the species is drawn from observations made in the vicinity of New London and New Haven, Connecticut, during 1930 and 1931.

The typical local distribution of *Melampus* in a salt marsh is shown in Fig. 2. From the zone between the

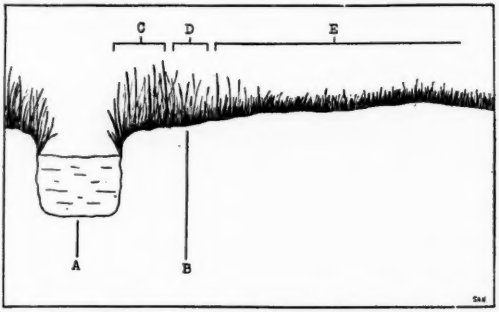

FIG. 2. Typical distribution of *Melampus bidentatus* in a salt marsh. A. Tidal creek. B. High tide line. C. Zone of coarse marsh grass. D. Zone of mingled coarse and fine marsh grass. E. Salt marsh itself (area of fine marsh grass).

low and high tide lines, Zone C, where the water rises to submerge the tall marsh grass, and where Fiddler Crabs (*Uca*) are usually numerous, *Melampus* occurs but sparsely. They are few or absent in Zone D, and begin to be numerous in the salt marsh above the point of the high tide line, B.

Although salt marsh snails are nocturnal feeders, some individuals emerge and may be found on the mud and the stems of grasses during the day, in shaded situations. Some few crawl about in the sunlight, but as a rule the direct rays of the sun are avoided. On damp, foggy or cloudy days many more of the snails become active, perhaps a quarter of the population of a given area. The majority, however, during the daylight hours, secrete themselves under stones, shells, bits of débris, or in dense tufts of marsh grass, and there remain quiescent with the body retracted far within the shell. About an hour after sunset they begin to emerge onto the bare mud areas in the marsh, which are covered with a thin greenish-brown slimy deposit. They also crawl up along the stems of the marsh grass, and over bits of débris, if these bear the same greenish-brown film.

During these periods of feeding the snails crawl slowly along, gathering in the slimy deposit just mentioned. Microscopic examination of this deposit, in the neighborhood of feeding individuals, showed it to be composed of diatoms, filamentous green algae and *Oscillatoria,* together with a gelatinous substance, and such fragments of the epidermal cells of the grasses as were being sloughed off or decayed.

Microscopic examination of the stomach contents of actively feeding individuals showed a large quantity of these epidermal cell fragments, together with bits of the filamentous algae noted before, and diatoms. Examination likewise of freshly voided excrement from feeding individuals (which appeared in minute vermiform masses on the mud and grass stems) exhibited fragments of the

same substances. From this, the food of the species is clear.

The eggs of the species (Fig. 3) are deposited on broken twigs, small stones, shells and grasses; and are

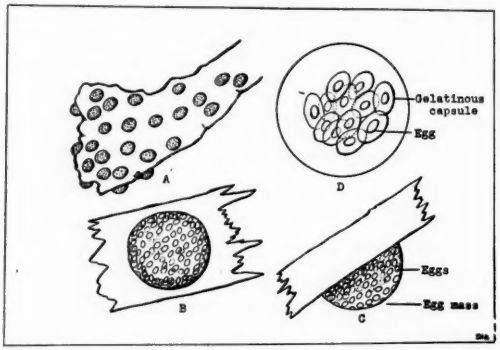

FIG. 3. Egg masses and eggs of *Melampus bidentatus*. A. Egg masses *in situ* on a broken twig found lying on the mud. B and C. Enlarged views of egg masses. D. Magnified portion of egg mass, showing the eggs.

laid in convex masses, each mass containing about two hundred eggs closely packed together in a transparent gelatinous matrix. The average major diameter of the egg masses is from one to two millimeters.

During the winter months the animals go into hibernation (though a few individuals may be found active during warm periods). While lying dormant during this season, the snails are closely packed together underneath shells, stones, dense tufts of marsh grass and holes in the mud. In such periods of inactivity the body is retracted far into the shell. The hibernating localities are well above the high tide line in the region of the short marsh grass, often on little hillocks in the marsh.

Melampus is preyed upon, and forms an important item in the dietary of small fishes, such as *Fundulus*. The stomach of *Fundulus pisculentus* caught at Woods Hole in July by Verrill contained no other food except large numbers of these snails. *Melampus* is also eaten by various marsh and aquatic birds, and also by song

sparrows, marsh wrens, swamp sparrows, red-winged blackbirds and other marsh-inhabiting species.

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COLOR AND PRIMENESS IN VARIABLE MAMMALS

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THE phenomenon of seasonal color change commonly seen in northern animals became of particular interest to the writer when it was found that primeness in all fur-bearing animals, save the albino, was solely dependent upon a blanching process of the hair-roots and entirely independent of dermal thickness or pigmentation. Subsequent investigation showed that the depigmentation process did not cease at the level of the epidermis, but that it was continued out into the proximal portion of the hair-shaft to a variable extent in different fur-bearing animals. The latter fact suggested the idea that the blanching of the jack-rabbit and Arctic white fox might merely be the outward evidence of an exaggerated state of this same physiological process.

Examination of the literature gave a very wide range of opinion as to the cause and nature of the seasonal change of color in these mammals. One interpretation of the process is that expressed by Allen (1894), Anthony (1928), Seaton (1928), Nelson (1918), and Pennant (1784), who with one accord state that the autumnal change of color in variable mammals (*Lepus americanus*) is due to a shedding of the pigmented summer fur and the growth of a white (albinotic) winter coat. On the other hand, Richardson (1829), Hadwen (1929), Merriam (1884) and Welch (1869) suggest that the change is not due to a shedding of the summer pelage, but that the existing coat lengthens and undergoes a blanching process, thus providing the winter coloration.

Both sides, with the exception of Hadwen and Merriam, apparently agree as to the manner in which the reversion to summer dress takes place, namely, that the

white winter fur is subsequently shed and replaced by the pigmented summer coat in the spring season.

The controversy as to the manner in which the process takes place has been waged over a century and a half, and the following extracts from the above authors indicate the opinions held by those on each side. Allen (1894) states:

(1) that the change of colour, both in autumn and in spring, is due to a change of pelage, and not, even in the fall, to a change in color in the hair itself. (2) Further, that this change is gradual, occupying many weeks, both in fall and in spring, and that while it may be doubtless more or less accelerated or retarded by temporary climatic conditions, it is not intimately connected with phases of weather, but is as regularly periodic as the seasons themselves. (3) That the method of change, as regards the parts first affected, is the reverse in spring of the order characterizing the autumnal change; in the fall the change beginning with the feet and ears, the sides of the nose and front of the head, which often become radically changed before the body is much affected; while, as regards the body, the change begins first at the base of the tail, and extreme posterior part of the body, working thence upwards toward the median line of the back and from behind anteriorly, the crown of the head and a narrow median line over the shoulders and front part of the back being the parts last changed. In the spring the order of change *is exactly the reverse*, the moult beginning on the head and along the median line of the anterior half of the dorsal region extending laterally and gradually to the ventral border of the sides of the body and posteriorly to the rump, and then later to the ears and down the limbs to the feet, which are the parts last affected, and which often remain but very little changed till the head and body have pretty completely assumed the summer dress.

Opposing this view Merriam (1884) states:

For in the fall the change certainly does occur, by a lengthening and blanching of the summer fur, the individual hairs changing color after the first fall of snow. This species, like the great majority of mammals, is clothed with two kinds of hair—a fine soft fur which densely covers all parts of the body, and longer, stiffer hairs, scattered through, and projecting beyond, the former. These long hairs are black in summer and white in winter. In the fall of the year when the change begins, they become white at the tips first, the black gradually fading from above downwards until the entire hair is white.

In the spring the process is reversed, the exposed portion of the long hair becoming black (though the extreme tips sometimes remain white until the change is far advanced), which color gradually extends downwards, at the expense of the white, until the entire hair is black. Sometimes the displacement of the white is temporarily interrupted, the two colors appear-

ing in alternate zones, and, during the latter part of March, when the body of the animal is still white, it is not uncommon to find hundreds of black hairs scattered over the back, many of them with extreme apices, and a narrow zone between the middle and base, white. In fall or early winter the soft fur becomes tipped with white, the white portion increasing somewhat in length and diameter. In spring a curious phenomenon takes place. The white portion of the fur loses its vitality, becoming brittle, and breaks off on slight friction, so that the animal in brushing through the undergrowth soon rids itself of it. As a rule the long hairs change first. Both in spring and fall the time of change seems to be governed by the presence or absence of snow and is not affected by temperature. It occurs independently of the moult, and the new hairs assume the prevailing color of the animal or the color towards which it is tending at the time of their appearance.

Probably the main reason for the great difference of opinion is due to the difficulty of trying to interpret all the conflicting phenomena proceeding simultaneously in these variable animals, which mask the more fundamental processes that are clearly seen when studying a pigmented non-variable animal such as the muskrat. Here the basic developments take place in a less complicated manner and show clearly the proper relationship of many features which it would be difficult to appreciate at first in a variable animal.

Color in non-variable fur-bearing mammals has been studied in detail by Hausman (1921), who, using muskrat hairs as a typical example of fur, has shown the histological basis for the variation in color throughout the hair-shaft, but this author failed to notice the marked difference in the distribution of the pigment in the proximal portion of the hair-shaft, depending upon whether the hair is taken from a prime or unprime area of the skin.

In hairs taken from an unprime pelt the pigment is continued down the hair-shaft into the root, and the condition of unprimeness in pelts may be shown to be due, not to pigmentation of the dermis or leather, but to the massed effect of the pigmented hair-roots. Conversely, primeness is due to the blanching of the hair roots; this process, however, does not terminate at the level of the epidermis,

but is continued out into the hair-shaft to a variable distance in different animals, and has been used by the author (1932) as the basis of a test for the detection of primeness in the pelts of *living* fur-bearing animals.

The present paper attempts: (1) To show the exact extent of variation in the priming process in a large number of fur-bearing animals, and to discuss its correlation with the nature and classification of these mammals; (2) to demonstrate the existing relationships between life cycle of the fur-hairs and the sequence of the blanching, priming and moulting processes.

The extent of blanching beyond the epidermis has been measured in the following animals, which include examples from three orders of mammals:

(1) Carnivora	(2) Otter (*Lutra canadensis*) Kuhl
	(3) Silver fox (*Vulpes fulva*) Desmarest
	(4) Mink (*Putorius vison*) Schreber
	(5) Lynx (*Lynx canadensis*) Kerr
	(7) Jaguarondi cat (*Felis cacomitili*) Baird
	(8) Cross fox (*Vulpes fulva*) Desmarest
	(11) Fitch (*Mustela putorius*) Boitard
	(12) Civet cat (*Arctigalidia fusca*)
	(13) Red fox (*Vulpes fulva*) Desmarest
	(15) Weasel (*Putorius noveboracensis*) Emmons
	(18) Arctic white fox (*Vulpes lagopus*)
(2) Rodentia	(1) Muskrat (*Fiber zibethicus*) Link
	(6) Black rabbit (*Lepus cuniculus*)
	(9) Grey squirrel (*Sciurus arizonensis*) Coues
	(10) Beaver (*Castor canadensis*) Kuhl
	(16) Varying hare (*Lepus americanus*) Erx
	(17) Jack-rabbit (*Lepus campestris*) Bach
(3) Marsupialia	(14) Common opossum (*Didelpys virginiana*) Kerr

Samples of under-fur hairs were obtained from prime pelts of the above-named animals by shaving them off close to the skin. Fig. 1 shows the relative degrees of depigmentation in the fur of these animals.

From a study of the figure it is evident that the extent of depigmentation is not related to the zoological classification, since the Rodents and Carnivores are found at both extremities. Again, there is no definite relation

between the extent of blanching and the length of fur, nor is there any corresponding proportion between the extent of this process and the width of the hairs, as Hausman (1924) has been able to demonstrate in the case of the "Scale Index."

Examination of the silver, cross and red fox hairs, which eliminates any chance of variation due to difference of species, suggests that density of pigmentation is the determining factor and also that this is a genetic character and is transmitted as such, for measurements show that the cross fox is situated midway between the silver and red fox, of which it is a hybrid.

There is a definite preponderance of semi-aquatic animals at the lower end of the chart, while the variable animals at the other extreme are all land mammals living in the northern hemisphere. Another interesting observation is that fur-bearers show a wide variation in the season at which the different mammals became prime. The pelt of the rabbit (*Lepus americanus*) is prime during December and January, while that of the muskrat at the other extreme becomes prime late in the spring, toward the end of March or in April.

It may be suggested that the variation in the time of priming can be explained upon the basis of the different mode of living found in these groups of animals. The former or semi-aquatic group is protected from the elements until spring, when its members are flooded out of their burrows, etc., while in the case of the land animals they are exposed to the sudden changes of temperature early in the winter season.

Examination of Fig. 1 shows the progression of depigmentation in a black, a snowshoe, and a jack-rabbit, lending support to the view that density of pigmentation is probably the major factor determining the amount of blanching in a given hair-shaft. It can be seen that the snowshoe rabbit occupies an intermediate position in showing the development of this feature, since the blanch-

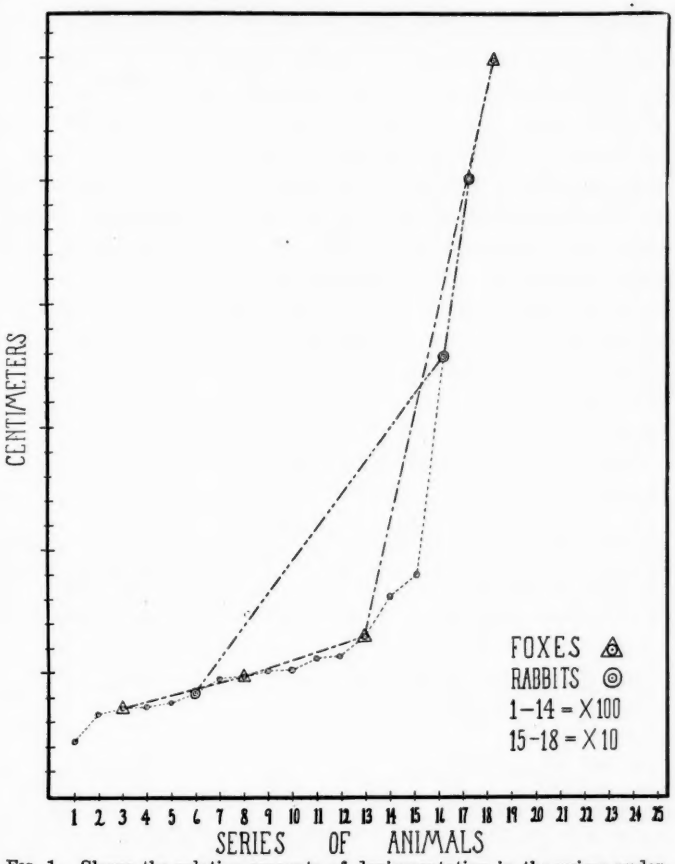

FIG. 1. Shows the relative amounts of depigmentation in the prime under-fur-hairs of a series of mammals (Key in text).

ing process takes place in such a manner as to leave the middle portion of the hair-shaft the last to become white. Reference to Fig. 2, III shows the intermediate state in the depigmentation process, corresponding to the winter pelage of the rabbit (*L. americanus*). Hence this animal does not show the priming process to as great an extent as the jack rabbit, etc., in which the process does not stop until the fur-hairs are completely blanched (Fig. 2, IV).

The seasonable color change therefore in variable animals may be attributed to an exaggeration of the priming process, which takes place annually in all other fur-bearers, to a variable but lesser extent, save in albinos.

Further evidence in support of this view is seen in the fact that the presence of the summer or pigmented coat in variable animals is coincident with the unprime state, while the blanched or winter pelage accompanies the prime condition of non-variable mammals.

Again, the sequence of blanching and the priming processes are the same—the mid-dorsal area is not only the last part of the skin to assume the winter coloration, but is also the last portion of a muskrat pelt to become prime.

Hadwen states with regard to the rabbit (*L. americanus*):

> Probably the most convincing proof that the change takes place in existing hairs is to be found in the skin itself, when the hair roots are examined. The fact that the roots cease to function as the hairs turn white, and that it is a progressive change, offers conclusive evidence that the alteration is destructive.

Again, in the same paper, with regard to the Arctic white fox, this author states:

> Portions of unprime white fox skins taken early in the winter show colour changes very similar to rabbits. Degenerating hair roots are found almost indistinguishable from those of a rabbit. It is evident that the alteration of color in the fur is preceded by loss of function on the part of the hair-roots.

We can not agree with this interpretation of the facts, however, that the blanching is due to the so-called degeneration of the hair-roots, since this process takes place in the roots of all fur-bearing animals which do not change color when they reach the prime state. Again, the change which takes place in the hair-roots, described in a previous paper (Gunn, in press), can not be looked upon as a destructive, but rather as a mature phase in the life cycle of the hair (Fig. 2, IV). The hair-roots

must reach this state before a pelt becomes prime, and it is well recognized that the length, density, sheen, texture and color of a pelage are seen in the optimum state only when the prime condition is reached. The nature of the priming and blanching process are therefore the same, the only difference being one of degree.

The relationship between a ripening process and the assumption of primeness is more clearly seen when the life cycle of the hair is studied.

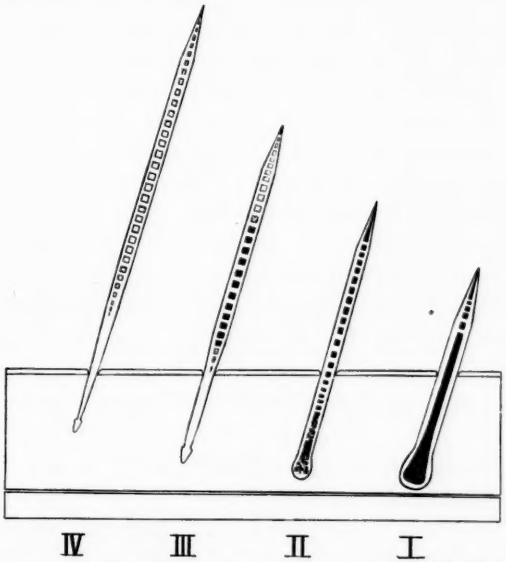

FIG. 2. Diagram showing four stages in the life cycle of an under-fur-hair of a variable mammal such as the jack-rabbit or Arctic white fox.

The different phases in the life of a fur-hair are shown in the diagram (Fig. 2). I represents a young hair which is densely pigmented down into the root. The massed effect of such hairs causes the pigmented condition seen on the fleshy side of an unprime pelt.

II represents a hair of the summer pelage in a variable animal, in which the melanin is not so densely congested in the root, and the hair has increased in length.

III shows a hair blanching, the root and tips preceding the intermediate portion of its shaft.

IV represents the totally blanched hair, typical of the winter pelage of the jack-rabbit, weasel and Arctic white fox, which has now reached its maximum length (the lengthening process referred to by Merriam, Welch, etc.) and may be considered as mature or prime. The mature phase lasts a definite length of time, and then this hair is shed. If it is not pulled out as probably is the case in the wild state, the old hair is pushed out upon the apex of the young hair growing beneath it and is eventually brushed off. It is now clear that the sequence of the growth of new fur, of the priming condition and of the moult is the same, and that the growth of new fur and the process of moulting proceed synchronously, but the prime phase is separated from these by a definite period of time. That different phases of the life cycle of the hair are present simultaneously during most of the year is seen in the prime and the unprime chart (Fig. 3).

This chart was constructed from the facts ascertained by studying a large number of muskrat pelts taken at different seasons of the year. Each concentric circle represents a cross-section of a pelt during a given season of the year:

I represents an early summer pelt in which only the ventral portion is unprime.

II is a mid-summer pelt, in which the ventral and lateral regions are unprime.

III represents a late summer pelt, the unprime condition prevailing throughout. Here the exact converse of the prime condition is seen.

IV is a fall pelt, in which only the ventral region is prime.

V represents the winter conditions of the pelt in which the ventral and lateral regions are prime, and the mid-dorsal area is unprime.

VI represents a spring pelt (the prime season of the muskrat) totally prime or devoid of pigmentation.

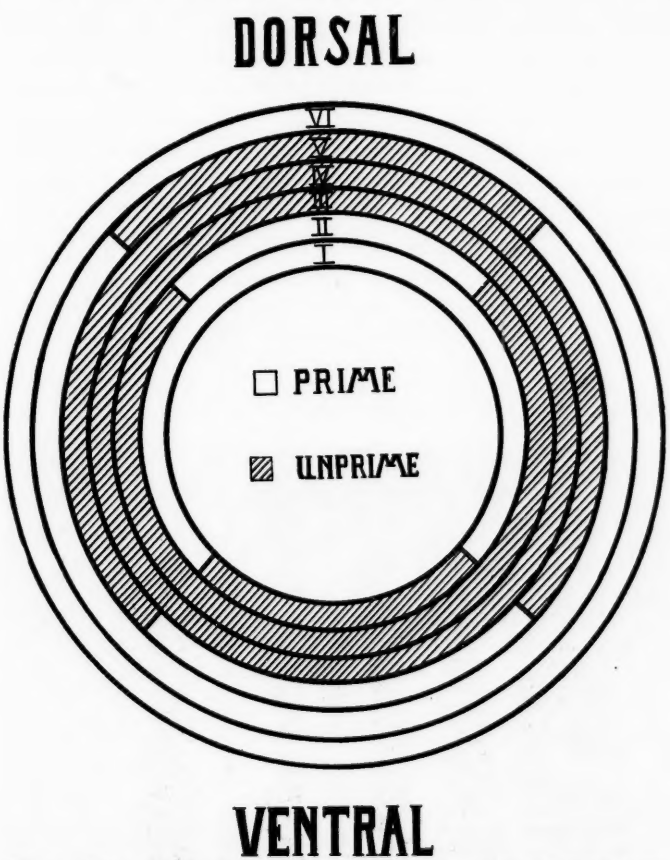

FIG. 3. Prime and Unprime Chart. The concentric circles represent transverse sections of pelts at different seasons of the year and show the sequence of the priming process.

This chart is also applicable to the rabbit, etc., if the seasons are adjusted, *e.g.*, the rabbit (totally prime during December) becomes prime earlier than the muskrat (totally prime during April), and likewise the other phases are seen proportionally earlier in the year. Referring to the chart it is evident that the different phases of the life cycle of the fur hairs are coexistent over the

body surface, except in the state of total unprimeness (III) and total primeness (VI), but it has been shown that where new fur is growing some shedding is present; hence this process does not take place simultaneously over the different body surfaces, but follows a definite sequence and is therefore present in a lesser degree throughout the year, save when the animal is totally prime. Moulting is at its height, however, when the pelt is totally unprime in the spring (III).

This explains the difficulty Hadwen (1929) encountered with regard to this condition, when he states,

> At no time during the year has the writer seen a heavy moult, such as one finds in tame animals, nor any evidence of matting as it occurs in long-

FIG. 4. Shows five stages in the change from summer to winter pelage in weasel pelts.

haired tame rabbits. Undoubtedly the greatest amount of hair is lost in spring, and a certain amount of the coat is loose and ready to fall out not long before the autumn change of color. Even after the hair has become white it is possible to pull out dead hairs which have all the appearance of belonging to the spring coat, they are black at the tip and have a light yellow zone. It is probable that these are the parti-colored hairs referred to by Allen. However, though some shedding goes on during the change, it represents only a very small percentage of the total hair covering. It never seemed probable that the rabbits would shed all their hair in the autumn and replace it during the early part of winter when they are in need of warmth. Furthermore it seems an impossibility for a pigmented animal like a rabbit to grow white hair unless it is an albino.

The lesser amount of moulting noted by Hadwen during the season when the coat was partly unprime is also objected to by fur-dressers when dressing unprime muskrat, beaver pelts, etc., (Gunn, 1932) and has been shown to be due to a remnant of the old coat in an unprime area of skin.

Hadwen (1929), Welsh (1869), Allen (1894), etc., have noted that the change in color follows certain areas with great regularity, as is also seen in the weasel (Plate I), but unfortunately they were unable to follow the sequence of the moult by means of the color change, owing to the fact that the rabbit remains white on its ventral surface throughout the year. The ventral region, however, becomes prime first and moults first. Not only is there definite evidence of this due to visible shedding in the ventral region, but if the fleshy side of the pelt be examined about February 1st, it is seen to be pigmented due to the growth of young hairs in this region. In other words, the cycle commences here again and is accompanied by moulting on this same surface of the body.

From a further study of the chart (Fig. 3) it would be expected that the period of total primeness would be of short duration, which agrees with the facts, for it is found that total primeness only lasts approximately one month (December in *L. amer.*). This is explicable, since the total condition only lasts from the time the dorsal surface becomes prime until the ventral surface shows

pigmentation again. The ventral areas become prime first and remain so while the sides and back reach this state in their turn. Hence, the dorsal surface is not prime long before the ventral region begins the cycle over again.

It has been suggested that the sequence followed by the priming process is due to the fact that the ground becomes cold in autumn before the sun loses its intensity, and therefore the maximum growth of fur is first required on the ventral surface. The same reasoning probably applies to the color change in variable animals, namely, that it is a modification of a phenomenon common to all fur-bearing animals, brought about through long inheritance, resulting in a better adaptation to environment, whether it be from protective coloration, from resistance to the rigors of winter or the heat and actinic rays of summer.

In summarizing it is evident:

(1) That the prime or mature condition of the fur occurs annually in all non-variable mammals (save albinos) and is coincident with the optimum attributes of the fur and with depigmentation of the hair-roots and shaft to a variable extent in different animals, and that autumnal color change is due to blanching of the summer coat or is merely an exaggeration of the same condition.

(2) That the pigmented summer coat of variable mammals corresponds to the unprime state and conversely the winter pelage of variable animals is comparable to the prime condition of non-variable animals.

(3) That the change from winter to summer coat in the jack rabbit, weasel and Arctic white fox is due to shedding of the white winter pelage and the growth of pigmented summer fur.

(4) That the same sequence is followed in the priming and blanching processes, in the moult, in the growth of new fur and therefore in the pigmentation of the pelt.

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SHORTER ARTICLES AND DISCUSSION

THE DISTRIBUTION OF GENES AMONG ISOMETRIC CHROMOSOMES

In a number of species, particularly of plants, the chromosomes of a set display no appreciable, or at least no marked, differences in size and form; the chromosomes are practically isometric and isomorphic. The 12 pairs of the tomato, for instance, are "short rods showing no distinct individuality" (Lesley, 1), a statement that is confirmed by the descriptions and illustrations of Winkler and other investigators. Vilmorin and Simonet (2) say, "la grosseur et la forme des chromosomes dans les celles mères des grains de pollen sont assez homogènes," and Jørgensen (3) found, in both somatic and meiotic divisions, that "the chromosomes are, as far as can be ascertained, identical in size and shape." A similar striking homogeneity is especially mentioned and clearly depicted as almost a general characteristic of the species of *Solanum* (2, 3), *Physalis, Capsicum, Atropa, Petunia, Salpiglossis, Lobelia, Linum* and *Campanula* (2). The chromosomes of *Primula sinensis* are "of very even size" (Sömme, 4). Winge (5) remarked that, in the sweet pea, "there is no difference, on the whole, in the size of the chromosomes," and that in *Antirrhinum majus,* another form of genetic interest, there are "eight chromosomes of uniform size." Such isomorphism is noted or shown by various authors in at least some species of *Aquilegia, Pentstemon, Godetia, Eschscholtzia, Rosa, Raphanus, Brassica* and *Vitis;* and a special search would undoubtedly find it wide-spread and common. In not a few insects the chromosomes are all "of practically the same size and shape" (6). Even in the fish, *Lebistes,* with 23 pairs, including an XY pair, "the chromosomes are very much alike" (7). It seems probable that, because of the interest attaching to individuality of chromosomes, especially of sex chromosomes, the species showing marked heterogeneity have been singled out and emphasized more than their numbers alone would justify. But pointing out the existence of these nearly isometric sets is not to be construed as denying or contradicting any fundamental tenet of the chromosome theory; the component chromosomes of such sets presumably possess as distinct a qualitative individuality as do those, for instance, in *Zea, Datura, Iris, Nicotiana,*

Drosophila or mammals, which are also more or less obviously quantitatively differentiated in size and form.

While the familiar studies with *Drosophila,* the pea, sweet pea, maize, snapdragon and *Datura* are general guides to the methods to be used and the results to be expected in linkage and chromosome works, it would seem that additional aids and guides might be developed for the geneticist and breeder undertaking a factorial analysis of those species, where size individuality in the complements is essentially lacking. Such analyses are likely to be made often in the future to test further the chromosome theory, to build up the objective data of a comparative genetics, and, in the applied field, to provide a foundation of knowledge for the use of the practical breeder.

In a genic analysis, the first gene studied will fall to some one chromosome, leaving the others unoccupied by known genes. As further factors are located, the hitherto unoccupied chromosomes will one by one acquire markers and gradually fill up with linked genes. At any stage in this process, it would often be interesting and helpful to know, and it is possible to predict for the species possessing chromosomes of approximately equal size: (1) (a) the proportion of chromosomes occupied or unoccupied by known loci; (b) the frequency of chromosomes carrying 1, 2, 3, 4 or more genes each; (c) the approximate number of genes it will be necessary to study to place at least one in each chromosome; (2) the proportion of factors that occur singly, or linked by twos, threes, etc.; and (3) the proportion of dihybrid combinations showing independent assortment, or linkage.

Theoretical Distribution of Genes among Isometric Chromosomes

Chromosomes of equal size (length) may be considered as approximately equal in gene content or number of loci, and for statistical purposes may be regarded as equal members of a larger group, the genom. The expected or probable distribution of genes, taken wholly at random, in such a set should obey certain statistical rules.

The theory involved is really that required to find the expected distribution of m objects (genes) in n boxes (haploid chromosomes), all of equal size and accessibility (9). This distribution is derived from the binomial, $(q+p)^m$, or $\left(\frac{n-1}{n}+\frac{1}{n}\right)^m$, where m

is the number of genes for which satisfactory linkage data are available, n is the haploid chromosome number, and p and q the chances of success or failure of any gene studied being in any one particular pair of chromosomes. That is, $p=\frac{1}{n}$ and $q=\frac{n-1}{n}$, and $p+q=np=1$. As n increases from 1, 2, 3 to 7 and 12, q rises from 0, $\frac{1}{2}$, $\frac{2}{3}$ to $\frac{6}{7}$ and $\frac{11}{12}$, and p falls from 1, $\frac{1}{2}$, $\frac{1}{3}$ to $\frac{1}{7}$ and $\frac{1}{12}$. When n is 2, then $p=q$, and the frequency distribution is symmetrical, but when n is 3 or more, q exceeds p, and the distribution is asymmetrical. Since the observed haploid chromosome number is commonly 6 to 12 or more, the initial asymmetry is characteristically very marked; when n becomes very large the law of small chances would apply (9).

The theory and derivation of this binomial and the most convenient methods of calculating its terms by logarithms have been described by Yule (9) and Johannsen (8). For valued helps and pertinent criticisms the writer is indebted also to Messrs. I. R. Pounder, C. P. Winsor and Sewall Wright.

APPLICATIONS TO LINKAGE STUDIES

(1) *The expected proportions of chromosomes occupied or unoccupied.* If we observed a great number of cases in which a series of m distinguishable genes were distributed at random, either simultaneously or consecutively, among n chromosomes of equal size, what would be the relative frequency of chromosomes containing 0, 1, 2, 3, 4 . . . m genes?

This distribution would be proportional to the terms of the binomial, $\left(\frac{n-1}{n}+\frac{1}{n}\right)^m$, and the probabilities of chromosomes being unoccupied, or occupied by 1, 2, 3, 4 . . . m genes are indicated by the numerical frequencies of the successive terms:

$$\left(\frac{n-1}{n}\right)^m + m\cdot\left(\frac{n-1}{n}\right)^{m-1}\cdot\frac{1}{n} + \frac{m(m-1)}{2}\cdot\left(\frac{n-1}{n}\right)^{m-2}\cdot\left(\frac{1}{n}\right)^2 + \frac{m(m-1)\,(m-2)}{2\cdot 3}\cdot\left(\frac{n-1}{n}\right)^{m-3}\cdot\left(\frac{1}{n}\right)^3 \cdots \left(\frac{1}{n}\right)^m$$

The full array of $m+1$ terms occurs with a minimum of $(n)^m$ distributions.

The same expectancies may be calculated by permutation methods. In general, if we ask the probability that a particular chromosome shall be found to contain just k out of the m genes,

this probability (corresponding to the relative frequency of any term of the binomial) may be calculated from the formula:

$$\frac{m!}{k!(m-k)!} \cdot \left(\frac{1}{n}\right)^k \cdot \left(\frac{n-1}{n}\right)^{m-k}$$

From the basic binomial the probability of a chromosome being occupied by at least one gene is $1-\left(\frac{n-1}{n}\right)^m$, and the mean number of occupied chromosomes is n times this value, or $n-\frac{(n-1)^m}{(n)^{m-1}}$. To be reasonably certain that markers will be found for all the chromosomes, the number of factors identified and placed must be such that $\frac{1}{n}$ well exceeds $\left(\frac{n-1}{n}\right)^m$; the expectation that no chromosome of the whole set shall be unoccupied by some one of the genes evidently can not be stated precisely in a simple way, but will lie between the not very wide limits, $1-\left(\frac{n-1}{n}\right)^m$ and $1-\frac{(n-1)^m}{(n)^{m-1}}$.

(2) *Distribution of the genes.* As regards the factors themselves, their mean number per chromosome is $\frac{m}{n}$, but they may occur singly or linked. The expected proportion of single markers and of genes linked by twos, threes, fours, etc., may be determined directly from the terms of $\left(\frac{n-1}{n}+\frac{1}{n}\right)^{m-1}$.

(3) *Proportion of dihybrid combinations showing linkage.* The probability that a pair of genes will be linked is clearly $\frac{1}{n}$. The total possible number of different pairings of m genes is $\frac{m(m-1)}{2}$. Combinations involving genes from different chromosomes assort freely, and those involving genes of the same chromosome should show linkage. The ratio of intra-chromosomal to the total possible number of combinations may be derived either from the binomial distribution or directly, the expected number of pairs showing linkage being $\frac{m(m-1)}{2} \cdot \frac{1}{n}$. The failure of genes far apart on a chromosome to show definite linkage tends to lower this proportion, but the practice of making linkage test combinations with only a few appropriately placed markers tends to raise the proportion greatly.

AGREEMENT BETWEEN OBSERVED AND THEORETICAL DISTRIBUTIONS

In the tomato, where n 12, and m represents the first 18 qualitative genes identified and studied in nearly all their possible dihybrid groupings, it now appears that one chromosome carries 4, one 3, three 2, five 1 and two none of these genes. These may be compared with the theoretical random groupings derived from $(\frac{11}{12}+\frac{1}{12})^{18}$ (Table 1).

TABLE 1

SHOWING THE CORRESPONDENCE BETWEEN EXPECTED AND OBSERVED DISTRIBUTIONS OF GENES IN THE TOMATO, PRIMULA AND SWEET PEA

		Frequency of chromosomes carrying							X^2	N = n−1	P
		0 gene	1 gene	2 genes	3 genes	4 genes	5 genes	6 genes			
Tomato											
expected	$(\frac{11}{12}+\frac{1}{12})^{18}$	2.5	4.1	3.2	1.5	0.5	0.2		10.	11	.53
observed		2.	5.	3.	1.	1.	0.				
Primula											
expected	$(\frac{11}{12}+\frac{1}{12})^{10}$	5.0	4.6	1.9	0.4	0.1			7.6	11	.75
observed[4]		6.	4.	1.	0.	1.					
Sweet pea											
expected	$(\frac{6}{7}+\frac{1}{7})^{10}$	0.4	1.2	1.8	1.7	1.1	0.6	0.2	3.1	6	.80
observed[11]		0.	2.	0.	4.	0.	1.	0.			

Of the 18 factors in the tomato 13 have been found linked and 5 single, where the probabilities on a random distribution were 13.9 and 4.1, respectively. Of the dihybrid combinations 7.8 per cent. were found linked, where 8.3 per cent. were anticipated. In general, the observed distribution appears by inspection to be consistent with the assumption of their random allotment among the approximately identical chromosomes. As a measure of the goodness of fit, should the conditions warrant so exact a procedure, the Chi-square test may be applied, when the number of genes is fairly large, since all equally probable combinations will yield the same X^2. Deviations are taken from the expected number of genes per chromosome, $\frac{m}{n}$. Thus the probability is .53 of getting a worse system of deviation than was observed in the tomato.

It would be interesting to apply similar tests to other cases where the basic conditions are reasonably well met. The chief difficulties encountered lie in the incompleteness of the objective data—not all the factor combinations having been tested, or the number of linked groups exceeding n, as in the pea (10)—and in the strong inclination of workers to select for first study genes which promise to belong to large linkage groups. The observations in Lathyrus (11), Primula (4) and possibly in Pisum (10) do not indicate any very significant departures from a chance distribution.

Summary

For the rather numerous species, whose chromosomes exhibit little or no size differentiation, it is suggested that some guidance in a genetic analysis may be found in calculating the theoretical distribution of groupings of m genes among the n pairs of chromosomes, by adaptations of the binomial formula, $\left(\frac{n-1}{n}+\frac{1}{n}\right)^m$. From these the geneticist may derive the expected proportion of chromosomes carrying 0, 1, 2, 3, 4 . . . m genes each; the approximate number of genes required to place at least one in each chromosome; the proportion of single and of linked genes; and the proportion of dihybrid combinations that will assort freely, or show linkage.

In the tomato the observed groupings of the first 18 factors identified and located seem consistent with the assumption of their random distribution among the 12 pairs of approximately equal chromosomes. The distribution of known loci in *Primula sinensis* and the sweet pea also accord reasonably well with expectation.

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AN EVALUATION OF SIZE GENES

IN a previous communication to this journal the author (1931) reported an association in heredity between size and coat color in mice. The data were derived from the back-cross generation of a cross between a strain of large *Mus musculus* carrying the recessive genes for dilution, brown and non-agouti and a race of small *Mus bactrianus* possessing the corresponding dominant allelomorphs. When the F_1 animals were mated to the recessive parent race, eight color classes of approximately equal numbers were obtained. A comparison of the dominant and recessive members of the three factor pairs involved disclosed an indubitable association between certain size and color characters. The size characters investigated included skull length, skull width (interorbital width), humerus, femur and tibia lengths, adult weight, body length, tail length and cranial capacity. Of these, the greater weight, humerus, femur and tibia lengths and body length, characteristic of the recessive *musculus* parent, were found associated with brown coat color derived from the same parent, while greater body and tail lengths likewise tended to be characteristic of those animals exhibiting the recessive gene for dilution. In those instances in which the mean difference between recessives and dominants

(brown, black and dilution, intensity) was as great as or greater than four times its probable error, genetic linkage between qualitative and quantitative characters was considered as demonstrated. It was not held that humerus length, for example, was determined entirely by a gene or genes linked with the gene for brown, but merely that such genes were partially determinative.

Although an interpretation making use of genetic linkage appears to fit the data satisfactorily, Castle (1932) has offered an alternative "non-chromosomal" explanation, which, however, it seems to me, is less tenable.

Since it was realized that the quantitative genes linked with b, for example, were responsible only in part for the respective size characters, an attempt to evaluate the size genes, to determine approximately the portion of the variability in the quantitative characters brought about by genes linked with the qualitative characters concerned, seemed advisable. I am indebted to Professor Sewall Wright for kindly suggesting the following method of analyzing the variance directly.

In general, the formula for the standard deviation due to b, B, for example, is $\sqrt{q(1-q)D^2}$, where q is the proportion in one class (browns), 1–q, the proportion in the other class (blacks) and D the difference between the means. The ratio of the variance, $q(1-q)D^2$, to the variance of the total (mixed) population (σ^2) gives the correct degree of determination except that no allowance is made for sampling differences. With numbers as large as ours, however, this can be ignored with the loss of practically little of significance.

Determination of Variance by Genes Linked with b, B

Character	Sex	No. of mice	Degree of determination
Humerus length	♂	152	12.56 per cent.
	♀	139	8.58 " "
Femur length	♂	151	9.25 " "
	♀	138	8.48 " "
Tibia length	♂	152	4.85 " "
	♀	139	6.56 " "
181st day weight	♂	153	8.33 " "
	♀	140	9.68 " "
Body length	♂	153	5.50 " "
	♀	140	5.48 " "

Determination of Variance by Genes Linked with d, D

Character	Sex	No. of mice	Degree of determination
Body length	♂	153	4.71 per cent.
	♀	140	4.71 " "
Tail length	♂	149	10.64 " "

A consideration of the cases in which linkage was observed, *i.e.*, cases in which the difference between the means of the recessive and dominant members of the factor pairs was as great as or greater than four times its probable error, gives the following results:

Of course the actual size factors may be responsible for a larger portion of the variance if not completely linked with the qualitative gene.

The above computations indicate that the size genes definitely located account for a distinct, although perhaps rather minor, portion of the variance in the respective size characters. It further appears probable that the latter are influenced as well by several or many genes situated in a number of chromosomes.

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THE INCIDENCE OF MAMMARY CANCER IN A CROSS BETWEEN TWO STRAINS OF MICE

THE report to be presented deals with a cross between a non-yellow (dilute brown) strain of mice high in the incidence of spontaneous carcinoma of the breast and a line of yellow mice lower in cancer incidence. In the latter line the type of cancer is usually sarcoma of various sorts. Data will be offered in a later paper, dealing more fully with the tumor-forming characteristics of both parent strains.

The object of the present report is to establish the existence of a clear difference in cancer incidence between the yellow and the non-yellow F_2 hybrids descended from the above cross.

It has long been recognized that most yellow mice have a type of general metabolism which differs from that of most non-yellows. This results in distinctly greater adiposity in yellow animals. The opportunity to contrast the incidence of mammary cancer in yellow F_2s and in their non-yellow sisters seemed therefore to be of interest.

In the cross to be recorded, virgin females were used in F_2 to determine the carcinoma incidence. This was done for two reasons. Females were chosen because the incidence of carcinoma of the breast in the stocks chosen is confined to that sex. Virgins were selected because there is evidence from the work of several investigators that the exercise of the reproductive function is a factor of great variability and complexity in contributing to the etiology of carcinoma of the breast in mice.

In the stocks used there is clear evidence that adenocarcinomas of the breast may appear as advanced stages in the development of adenomas. These more or less benign tumors are therefore included among the cancer class in the data presented.

There was a total of 260 F_2 virgin females which lived to an age sufficient to allow them to be included as critical data in determining cancer incidence. Of these 136 were yellow and 134 non-yellow. Among the two classes the incidence of cancer of the breast was as follows:

	Cancer	Non-cancer	Per cent. cancerous
Yellows	53	83	38.97 ± 2.81
Non-yellows	80	54	59.70 ± 2.85

The difference (20.73 ± 4.00) is 5.18 times its probable error. There is no question, therefore, that a significantly higher proportion of non-yellows than of yellows form cancer of the breast in this particular hybrid generation.

The next matter of interest is to attempt to obtain some information as to the cause of the difference.

The two explanations which seem to be the most probable are (1) that genetic linkage exists between a gene determining high incidence of mammary cancer and the gene for the non-agouti

(a) allelomorph of yellow (A^y), and (2) that there is something in the actual metabolism of a yellow (A^y) mouse which makes that animal unfavorable to the development of mammary carcinoma.

Data are not at present available to decide finally between the two possibilities. Certain evidence bearing on them may, however, be mentioned.

If the physiological explanation is the correct one it might easily follow that yellow mice would have a different life span and so might not be strictly comparable to non-yellows. Comparison in respect to this factor, however, shows that no significant difference exists in this respect between yellows and non-yellows as a whole. If, however, yellow cancerous mice are contrasted with non-yellow cancerous animals it is found that the mean age at death of the yellows is 476.0 ± 14.26 days, while that of the non-yellows is 550 ± 13.62 days. This difference is 3.7 times its probable error. If the difference is significant, as it may well be, it becomes important to compare also the age at death of non-cancerous yellows and non-cancerous non-yellows. When this is done the mean age of the yellows is 599 ± 11.48 days and for the non-yellows 628 ± 13.00 days. The difference is only 1.6 times its probable error and is not significant.

It is clear, therefore, that the evidence from these data shows no physiological handicap as such to the formation of cancer of the breast in the yellow mice. Provided an individual yellow mouse is going to have cancer it actually dies of it significantly earlier than do the non-yellows. This signifies for the yellows either earlier incidence of cancer or greater malignancy or both. Either or both these facts tend to militate against the probability of the existence of any general metabolic factor discouraging to cancer formation and peculiar to yellow animals.

A certain amount of supplementary evidence as to the comparative malignancy of tumors of the breast in yellow and in non-yellow hybrid mice is also available. Since adenomas are of a lower grade of malignancy than carcinomas a tabulation of the comparative incidence of this type of neoplasm and of carcinomas in yellows and in non-yellows can be made. If the yellows have a general metabolic factor which decreases the likelihood of malignancy, these figures should show it. Actually of the 53 tumors in yellows 44, or 83 per cent., are carcinomas, while 17 per cent. are adenomas. Of the 80 tumors in non-yellows 57,

or 70.4 per cent., are carcinomas and 29.6 per cent. are adenomas. The figures certainly show no decrease and possibly an increase in malignancy in the tumors of yellow animals. This evidence suggests further the improbability that a general metabolic factor is involved.

With these facts in mind we may conclude that a careful breeding experiment, using agouti (A) rather than yellow mice (A^y) as the low cancer strain, should be carried out. This should suffice to show whether linkage between high incidence of cancer of the breast and the non-agouti (a) locus exists.

Whether it does or not, a difference in incidence of mammary cancer between yellows and non-yellows is already clearly established and forms the first evidence of an important interrelationship between a color variety of mice and the spontaneous incidence of mammary cancer.

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RECOMBINATION AND CROSSING-OVER

THE interpretation of the term "percentage of recombination" as "percentage of new combinations" (Hutt, AM. NAT., 66: 274) is not only entirely correct, it is orthodox as well. "Recombination" has been consistently used as synonymous with "new combination" throughout; for example, in the explanation of Drosophila symbolism given by Bridges and Morgan (Carnegie Pub. No. 327, p. 9):

> When linked genes enter a cross certain individuals in the second generation may show new combinations of the characters that entered from the different parents. Thus, if Dichaete is crossed to pink, and the F_1 female is back-crossed to a pink male, most of the flies are of the two original types, Diachaete or pink; but a small number of the offspring are both Dichaete and pink or neither (*i.e.*, wild type). These two latter classes are called "recombination classes" and the "percentage of recombination" may be found by dividing the sum of the recombination classes by the total number, and multiplying this decimal fraction by 100. . . . The use of the term "recombination" in this technical sense is a shortening of the full term "recombination of linked characters."

But while Hutt agrees with this synonymy of new combinations with recombinations, as this term has been defined and used, he is of the opinion that on etymological grounds this meaning, in any sense of the word recombinations, is not legiti-

mate; that in the true interpretation this term is applicable only to the genotypes and phenotypes which are the same as those of either parent. It sometimes happens that there is more than one well-defined true meaning of a prefix, and "re-" is a good example of this. According to the Century Dictionary, "re-" has, besides its meaning of "back" (illustrated in such words as remit, reflex), a meaning of "against" (react, rebel, resist). Besides the meaning "restoration to a former state" (reintegrate, reset), it has the meaning "transition to an opposite state" (revolution, recant, reform). The meaning "repetition of a former act" is evident in the words rearrange, redeal, redye, remarry, reword, rewrite. It should be noted that it is the act which is repeated, while the objects acted upon or with may be entirely new (as in remarry); or the result of the action upon old objects may be something new (as in rearrangement, redeal, redye). The word "replace" means either restoration to a former state (to replace a key upon its hook) or transition to a new state (to replace a hydrogen by a carboxyl). While "recombine" is not exhaustively defined, its close analogy to "rearrange" (to arrange anew, make a different arrangement) and the thoroughly accredited use of "re-," with the connotation of transformation to a new state or result, make it entirely permissible for "recombination" to be employed to designate new or different combinations, especially if its use is in a technical field and is prefaced by a clear statement of its intended significance.

There is an objection to be raised from another point of view, namely, that "recombination" had been already used in genetics, in connection with the 9:3:3:1 ratio of non-linked characters. This priority was of course known, but in the early days when recombination was used in connection with the F_2 ratios, the emphasis was entirely upon the end result, namely, the classes of individuals, and the distinction as to the recombinations being produced by reassortment or by crossing-over had not arisen. In the definition of "recombination" by Bridges and Morgan, quoted above, it is recognized that the recombination of linked characters is a special use of the term instead of its general use, which did not specify the method of recombination as through reassortment rather than through crossing-over. That it was not restricted to non-linked characters in usage is illustrated by the other prior use of the word by Lotsy, where again the emphasis was upon the new forms which originate from the reshuffling and new combinations of the old genes.

Lotsy would not throw out of consideration as recombinations those cases in which the original two genes were carried by the same chromosome (hence recombination through crossing-over). Both of these early uses were *general* and did not exclude the *special* use of the term in connection with one or with the other mechanism of production of the recombinations.

As a matter of fact, the only cases where it would be uncertain as to whether the term recombination were being used in the one rather than in the other special sense are exactly those in which it isn't known whether the mechanism is reassortment or crossing-over, and hence the general sense is needed. Such cases are where the percentage of recombination is not a statistically significant departure from the 50 per cent. corresponding to random recombination.

One of the strong points in favor of the term "recombination" is exactly that it permits a clear separation of two categories, one the observed result (a series of classes of individuals) and the other a mechanism behind that seriation (reassortment or crossing-over). It was not recognized in the early days of linkage study that this distinction should be made and kept sharp. As a result it was almost impossible to be clear in the explanation of the relations of "map-distances" to the percentages observed in experiments. The "linkage values" or better the "crossover values" of the early papers meant indiscriminately now map-distances and now observed percentages. It could not be made a general law that "crossover values are additive" as long as "crossover values" could mean the "percentages of recombination of the characters." For example, the percentage of recombination for white and miniature was approximately 33, and for miniature and rudimentary approximately 18. If these be added, the result (51) is in excess of the value (42) observed for white and rudimentary. The common side-step was to say that the "apparent" crossover value was 42, while the "real" crossover value was 51. But as soon as one defines the observed percentage as a "percentage of recombination" and reserves the term "crossover value" for the map distances all becomes clear.

Whenever one uses the term crossing-over one refers now to the mechanism behind the recombination of the characters or of the genes for the characters. Crossing-over is something which occurs to the chromosomes at a particular point along their length. If one crossover falls *between* the loci for two pairs of characters then these characters will emerge as recombinations.

But the number of crossovers may exceed the number of recombinations per hundred gametes, for each double crossover leaves in their original alignment all loci outside the region between the two crossovers.

Now map distances and crossover values (synonymous) are always additive (aside from errors in experimental determination) while percentages of recombination are related through a complex formula involving the coincidence index for the special section considered. The increase in recombination percentage, as successively longer sections are considered, is not additive and approaches 50 per cent. as its limit. It becomes apparent that the simplest method of predicting the percentage of recombination corresponding to a given map distance, or, conversely, the map distance corresponding to an observed percentage of recombination, is through special correction curves based on all available information as to the specific situation for each specific region of each chromosome. Such a set of correction curves for the third chromosome is given on page 12 of the above quoted paper by Bridges and Morgan. Recombination is always expressed as a percentage, and map distance or crossover value never as a percentage but always as a number of units. This unit is carefully defined as that length of chromosome within which on the average one case of crossing-over occurs for each hundred gametes tested. The term "linkage value" should be dropped, since linkage is evaluated in crossover units, just as interference is now expressed in the index of coincidence.

The study of recombination percentages for linked characters is simply a means to the end of studying crossing-over frequencies and distributions. The center of interest is the crossing-over relations; hence it is emphasizing the symptomatic result rather than the underlying mechanism when one speaks of "recombination in fishes," rather than of "crossing-over in fishes." In his objection to this usage, Hutt is entirely right; but he is entirely wrong in supposing that the only term needed is crossing-over. Besides "percentage of recombination," the synonyms "percentage of new combinations" and "percentage of separation" have been used more or less in the Drosophila work. But the term "recombination" has the advantage over these other equally valid terms in compactness and in smoothness of its use in various situations by its ready transformation into the corresponding verb and adjective.

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